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Neue fossile Rüsselkäfer (Coleoptera: Curculionidae) aus dem Eozän des Baltischen Bernsteins und der Grube Messel bei Darmstadt

New Eocene weevils (Coleoptera: Curculionidae) from Baltic amber and from Messel oil shales (Darmstadt, Germany)

Joachim Rheinheimer

Zusammenfassung

Die fossilen Rüsselkäfer *Palaeoalatorostrum schaali* n. gen. n. sp., *Palaeocneorhinus messelensis* n. gen. n. sp., *Palaeocrassirhinus messelensis* n. gen. n. sp. und *P. rugosithorax* n. gen. n. sp. werden aus dem Ölschiefer von Messel (Eozän), *Protoceletes wolfschwenningerae* n. gen. n. sp. und *Electrotribus erectosquamata* n. sp. aus dem Baltischen Bernstein (Eozän) beschrieben. Die systematischen Zusammenhänge und die Beziehungen zu rezenten Taxa werden diskutiert.

Abstract

The fossil weevils *Palaeoalatorostrum schaali* n. gen. n. sp., *Palaeocneorhinus messelensis* n. gen. n. sp., *Palaeocrassirhinus messelensis* n. gen. n. sp., and *P. rugosithorax* n. gen. n. sp. from the Messel oil shales (Eocene), *Protoceletes wolfschwenningerae* n. gen. n. sp. and *Electrotribus erectosquamata* n. sp. from Baltic amber (Eocene) are described as new. Systematic implications and relations to modern taxa are discussed.

Keywords: Curculionidae, Eocene, Messel, Baltic Amber.

1. Einleitung

Seit dem Mesozoikum bekannt (Arnoldi et al. 1977) wurden Rüsselkäfer (Curculionidae) in verschiedenen Formationen des Tertiärs an etlichen Lokalitäten gefunden. Besonders gut erhalten sind sie im Baltischen Bernstein (Voss 1953, Kuschel 1992). Auch in jüngeren tertiären Schichten gibt es etliche Rüsselkäferarten (z.B. Heer 1847, Scudder 1893, Zherichin 1992, Poinar & Poinar 1999).

Die Grube Messel ist mit ihrem Ölschiefer aus dem Unteren Mitteleozän (Lutetium) eine Fossilienfundstätte von Weltrang, aus der von Säugetieren bis zu den Insekten Tiere aus vielen verschiedenen Gruppen sowie Pflanzen stammen. Die große

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Artenfülle und der gute Erhaltungszustand ermöglichen einen umfassenden Einblick in diesen tertiären Lebensraum (z. B. SCHAAL & ZIEGLER 1992). Seit MEUNIER (1921) wurden aus Messel bereits verschiedene Insektenfamilien untersucht, wobei die Käfer die größte Gruppe stellen (LUTZ 1990). Von den größeren Familien wurden z. B. die Schnellkäfer (Elateridae) von TRÖSTER (1994) ausführlich studiert, der auch eine Zusammenstellung der Literatur angab. Die Rüsselkäfer sind mit über 600 Stücken sehr reich vertreten, blieben bisher aber noch unbearbeitet.

Der eozäne Baltische Bernstein, dessen Alter mit etwa 40–54 Millionen Jahren angegeben wird (WEITSCHAT & WICHARD 1998), ist die wichtigste Quelle für sehr detailliert erhaltene, fossile Rüsselkäfer aus dem frühen Tertiär, von denen bisher etwa 20 Arten beschrieben wurden (VOSS 1953, ZHERIKHIN 1971, VOSS 1972, WANAT & BOROWIEC 1986, KUSCHEL 1992, KUSKA 1992). Diese stellen nach eigenen Untersuchungen mehrerer Museums- und Privatsammlungen aber nur einen kleinen Teil der vorhandenen Arten dar. Bisher lagen mir etwa 100 Arten vor. Die tatsächliche Zahl dürfte aber deutlich höher liegen, da bedeutende Sammlungen z. B. in Osteuropa, Japan und Amerika bisher nicht einbezogen werden konnten.

Da beide Fossilienvorkommen aus einem etwa vergleichbaren Zeitraum stammen, liegt ein gemeinsames Studium nahe, um schließlich zu einem besseren Verständnis der früh-tertiären Käferfauna zu kommen.

Heute stellt die Familie der Rüsselkäfer mit weltweit etwa 60000 beschriebenen und noch viel mehr unbeschriebenen Arten die größte Tierfamilie dar. Auch in Mitteleuropa ist sie mit fast 1300 Vertretern gut repräsentiert und nach den Kurzflüglern (Staphylinidae) die zweitgrößte Gruppe. Ihre Lebensweise ist mit wenigen Ausnahmen phytophag, wobei Spezialisten und polyphage Tiere fast alle Pflanzenfamilien und alle Pflanzenteile nutzen können, so dass die meisten terrestrischen Lebensräume besiedelt werden (z. B. RHEINHEIMER 2002).

Dank

Frau Dr. K. WOLF-SCHWENNINGER, Staatliches Museum für Naturkunde Stuttgart und Herr Dr. S. SCHAAL, Forschungsinstitut Senckenberg, haben mir in freundlicher und dankenswerter Weise die von ihnen betreuten Sammlungen zugänglich gemacht. Frau Dr. K. WOLF-SCHWENNINGER präparierte außerdem die untersuchten Bernstein-Funde. Den Herren Dr. A. RIEDEL, Naturkundemuseum Karlsruhe, Dr. R. BÖTTCHER und Dr. W. SCHAWALLER, Naturkundemuseum Stuttgart, danke ich für wichtige Hinweise.

2. Material und Methoden

Die Fundstücke aus dem Ölschiefer befinden sich in der Sammlung des Forschungsinstitutes Senckenberg (FIS), Forschungsstation Grube Messel. Fundort ist die Grube Messel bei Darmstadt, Hessen, Deutschland. Sie stammen aus dem Mittleren Eozän, Unteres Lutetium, MP 11, Messel-Formation (Stratum typicum für die hier beschriebenen Taxa).

Die nach der Aufspaltung des Gesteins sichtbare Seite ist freigelegt. Zur Konservierung des wasserhaltigen Gesteins werden sie unter Glycerin aufbewahrt. Da der Tonstein sehr dunkel ist, wurde mit starken Blitzgeräten photographiert und die Abbildungen digital nachbearbeitet. Sie erscheinen deshalb heller als im Original.

Die Fossilien sind dorso-ventral oder lateral flachgedrückt und weniger als einen Millimeter dick. Dadurch können sich die Proportionen der häufig stark gewölbten

Tiere erheblich verändert haben. Die Längenverhältnisse werden demnach nur qualitativ angegeben und müssen vorsichtig interpretiert werden. Berücksichtigt man dies, so weisen viele Stücke trotzdem im Habitus große Ähnlichkeit zu rezenten Arten auf.

Häufig sind nicht alle taxonomisch wichtigen Merkmale wie Fühler, Beine und Mundwerkzeuge verfügbar. Nicht immer gibt es Funde sowohl in dorsaler als auch in lateraler Lage oder diese sind einander nicht vollkommen sicher zuzuordnen. Deshalb muss bei der systematischen Einordnung der fossilen Rüsselkäfer – außer beim Baltischen Bernstein – häufig auch der Habitus mit herangezogen werden. Dies ist bei einer so formenreichen Insektenfamilie schwierig. Trotzdem ist eine Zuordnung auf der Basis der vorhandenen Merkmale zu einer Gattung sinnvoll, weil dadurch die weitere Bearbeitung und die Klassifizierung zukünftiger Funde wesentlich erleichtert werden. So ist es möglich, die jeweils verwandten Taxa effizient in der Literatur aufzufinden und für die Untersuchung mit heranzuziehen. Dies ist besonders bei einer großen Familie wie den Rüsselkäfern von Bedeutung.

Die Fundstücke aus dem Baltischen Bernstein befinden sich in der Sammlung des Staatlichen Museums für Naturkunde Stuttgart (SMNS).

3. Systematischer Teil

Wegen der großen Artenvielfalt ist die Systematik der Rüsselkäfer insgesamt noch ungenügend ausgearbeitet, so dass auch bei den rezenten Taxa viele Gattungen und Tribus nicht endgültig platziert sind. Entsprechend befindet sich dieses Arbeitsgebiet noch im Fluss und neue Erkenntnisse führen immer wieder zu veränderten Auffassungen hinsichtlich der systematischen Beziehungen (KUSCHEL 1995, ZHERICHIN & GRATSHEV 1995, WINK et al. 1997, MARVALDI & MORRONE 2000, MARVALDI et al. 2002). In der vorliegenden Arbeit wird das neueste System verwendet, das weltweit alle rezenten und fossilen Taxa bis zur Gattung erfasst (ALONSO-ZARAZAGA & LYAL 1999).

Aus Messel werden hier zunächst die Vertreter der Unterfamilie Entiminae vorgestellt. Die übrigen Gruppen befinden sich noch in Bearbeitung. Hinzu kommen Bernstein-Fossilien aus weiteren Unterfamilien.

3.1. Funde aus Messel

Unterfamilie Entiminae SCHOENHERR, 1823
Tribus Otiorhynchini SCHOENHERR, 1826

Gattung *Palaeoalatorostrum* n. gen.

Typus generis: *Palaeoalatorostrum schaali* n. gen. n. sp.
Derivatio nominis: παλαιός (griech.) alt, alatus (lat.) geflügelt, rostrum (lat.) Rüssel.

Diagnose. – Fühlereinlenkung an der Spitze des breiten Rüssels seitlich stark vorstehend; Rüsselrücken hier deutlich breiter als an der Basis des Rüssels, wo er kaum halb so breit ist wie ein Auge; Fühlerschaft unvollständig erhalten, schlank, am Ende gerade. Die rundlichen Augen stehen an den Seiten des Kopfes, der hinter den Augen eine deutlich abgesetzte, glattere Skulptur aufweist. Halsschild glatt, unbehaart, spärlich und fein punktiert, ohne Augenlappen. Flügeldecken etwas länger als zusammen breit, in der Mitte parallelseitig, mit teilweise etwas undeutlichen Punktstreifen und einer verrundeten Schulterbeule. Vorderschienen schlank, etwa so lang wie Kopf und Halsschild zusammen; Schenkel ungezähnt und die Klauen an der Basis getrennt.

Beziehungen. – Nach dem Bau des Kopfes mit einem breiten Rüssel und nach den oben offenen Fühlerfurchen gehört diese Gattung in die Unterfamilie Entiminae. Eine Assoziation mit der Tribus Otiorhynchini legen die seitlich vorstehenden Fühlereinlenkungen und die fehlenden Augenlappen nahe. Außerdem weisen die Tarsen, soweit erkennbar, an der Basis getrennte Klauen auf.

Die Tribus Celeuthetini aus Neuguinea zeigt ähnliche Merkmale (MARSHALL 1956). Sie kann von den Otiorhynchini an der Form und Beschuppung des Apex der Schienen unterschieden werden, was aber selbst bei rezenten Tieren oft schwer erkennbar ist. Beide Tribus sind durch ihre heutige Verbreitung weit voneinander getrennt; ein gemeinsames Vorkommen in Mitteleuropa im Eozän wäre aber möglich.

Obwohl die genaue Zuordnung demnach unsicher bleibt, wird diese Gattung vorläufig in die Nähe der Gattung *Otiorhynchus* GERMAR, 1824 gestellt, mit der sie in den Merkmalen des Rüssels, der Beine und Flügeldecken übereinstimmt. Zum Vergleich kann der rezente *Otiorhynchus alpicola* BOHEMAN, 1843 aus den Alpen dienen (Abb. 1), der außerdem Gemeinsamkeiten im Bau des Kopfes und in der Skulptur der Flügeldecken zeigt, die aber seitlich stärker gerundet sind. Außerdem ändert sich bei dieser Gattung die Skulptur des Kopfes nicht abrupt hinter den Augen. Ähnlich ist auch der südafrikanische *Sciobius* SCHÖNHERR, 1823, dessen Rüssel aber an der Fühlereinlenkung viel weniger erweitert ist.

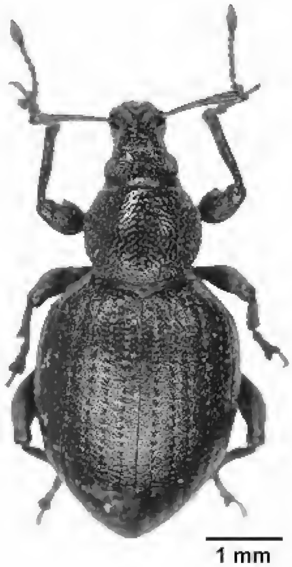

Abb. 1. *Otiorhynchus alpicola* BOHEMAN, 1843; rezent, Alpen (Sammlung RHEINHEIMER).

Palaeoalatorostrum schaali n. gen. n. sp.
Abb. 2–4

Holotypus: MeI 5575 (Abb. 2); FIS, Forschungsstation Grube Messel.

Locus typicus: Grube Messel, Grabungsstelle E8/9 (Grabungsjahr 1996).

Stratum typicum: Messel-Formation, Fundbereich: 0–0,28 m unter Leithorizont α.

Paratypen: MeI 1196 (Abb. 2, Fundort: Grabungsstelle 5 (E15), Grabungsjahr 1984, Fundbereich: ca. 2 m über bis 2 m unter Leithorizont α); MeI 4784 (Abb. 3, Fundort: Grabungsstelle E8/9, Grabungsjahr 1995, Fundbereich: 1,55–1,75 m unter Leithorizont α); FIS, Forschungsstation Grube Messel.

Derivatio nominis: Diese Art ist Herrn Dr. S. Schaal, Leiter der Abteilung Messelforschung am Forschungsinstitut Senckenberg, gewidmet.

Diagnose. – Siehe Diagnose der Gattung.

Beschreibung. – Holotypus (Abb. 2): Länge: 6,5 mm, in Dorsalansicht erhalten.

Integument: Das gesamte Fossil einschließlich der teilweise frei liegenden Tergite ist blaumetallisch überlaufen. Bemerkenswert ist, dass heute in der Unterfamilie Entiminae vergleichsweise wenige Vertreter mit metallischen Strukturfarben vorkommen (z. B. *Pachyrhynchus*, Tribus Pachyrhynchini). Oft werden allerdings metallische Oberflächen durch entsprechende Schuppen gebildet.

Kopf: Die Augen stehen seitlich halbkugelig vor, die Stirn zwischen den Augen ist etwa eineinhalbmal so breit wie die Augenlänge, schwach in Längsrichtung skulptiert. Der Kopf ist unmittelbar hinter den Augen dorsal deutlich eingeschnürt, dahinter fein quergerieft. Der Rüsselrücken ist an der Basis weniger als halb so breit wie die Augen, nach vorn ist er erweitert. Der Rüssel ist doppelt so lang wie die Augen und unterhalb der Fühlereinlenkung seitlich stark verbreitert. Die Fühler sind nicht sichtbar.

Halsschild: Er ist deutlich breiter als lang, wobei dies durch die Einebnung bei der Fossilisierung verfälscht sein kann; er ist etwas verdreht eingebettet. Die Oberseite ist glatt, fein punktiert, die Punkte sind um mindestens einen Durchmesser vonein-

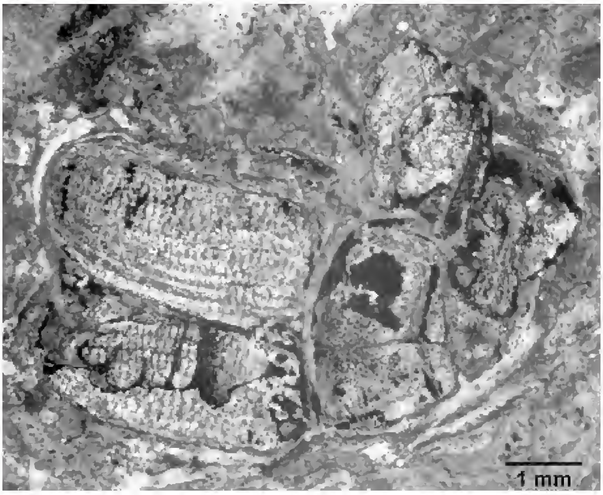

Abb. 2. *Palaeoalatorostrum schaali* n. gen. n. sp., Holotypus; Mittleres Eozän, MP11, Grube Messel; MeI 5575 (FIS, Forschungsstation Grube Messel).

ander entfernt. Die vollständige, feine Mittellinie tritt bei den Entiminae seltener auf und könnte eventuell bei der Einebnung des gewölbten Halsschilds als Riss entstanden sein. Dafür spricht auch, dass eine Mittellinie bei MeI 4784 nicht zu erkennen ist. Die Seiten des Halsschilds sind nach vorn leicht gerundet verengt. Ein schwacher Quereindruck am Apex könnte ein Artefakt sein.

Flügeldecken: Die Flügeldecken sind etwas länger als zusammen breit, fast parallelseitig, besonders auf der Oberseite mit kräftigen Längsstreifen von der Breite der Zwischenräume. Die Punkte der Streifen sind in der Mitte um einen Durchmesser voneinander entfernt. Die Granulierung der Zwischenräume lässt die Streifen an den Seiten zunehmend unregelmäßig erscheinen. Der Nahtstreifen ist vertieft. Durch die Unvollständigkeit des Fossils in diesem Bereich ist das Schildchen nicht zu erkennen.

Beine: In Teilen erhalten sind beide Vorderbeine sowie das linke Mittelbein. Die Schenkel sind keulenförmig verbreitert, vermutlich zum Teil durch die Einebnung bei der Fossilisierung, fein und ziemlich dicht punktiert. Die Vorderschienen sind etwa so lang wie der Halsschild, von 2/3 Augenbreite, innen mit fast gerader, ungezähnter Kante, außen leicht gebogen. Das dritte Tarsenglied des Mittelbeines ist gelappt, breiter und kürzer als das zweite. Das Klauenglied ist länger als Glied 3. Es ist nicht zu erkennen, ob die Klauen an der Basis verwachsen sind.

Paratypen: Sie sind insgesamt weniger gut erhalten, liefern aber zusätzliche Details.

Bei MeI 4784 (Abb. 3) ist der Kopf in Seitenlage eingebettet. Teile der Fühler sind zu erkennen. Der linke Fühlerschaft tritt hinter der abgewandten Seite des Kopfes

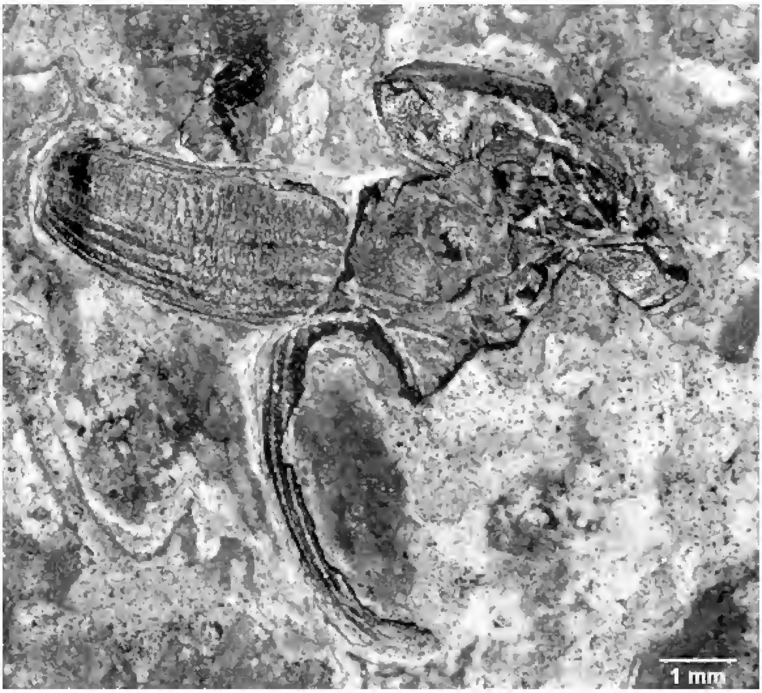

Abb. 3. *Palaeoalatorostrum schaali* n. gen. n. sp., Paratypus; Mittleres Eozän, MP11, Grube Messel; MeI 4784 (FIS, Forschungsstation Grube Messel).

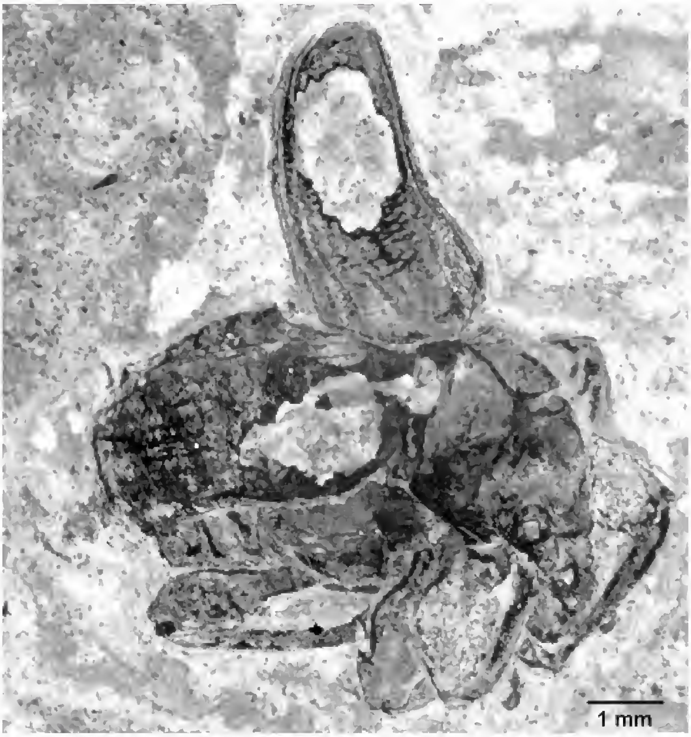

Abb. 4. *Palaeoalatorostrum schaali* n. gen. n. sp., Paratypus; Mittleres Eozän, MP11, Grube Messel; MeI 1196 (FIS, Forschungsstation Grube Messel).

hervor und ist bis zum Ende gerade. Beide Klauenglieder der Vordertarsen sind sichtbar (das rechte liegt neben dem Ende der linken Vorderschiene). Die Klauen erscheinen an der Basis getrennt. Eine Mittellinie des Halsschilds ist bei diesem Exemplar, wahrscheinlich wegen der seitlichen Einbettung, nicht zu beobachten. Der Halsschild ist seitlich hinter den Augen gerade, ohne Augenlappen.

MeI 1196 (Abb. 4) zeigt einen Hinterschenkel, der zum Ende keulenförmig erweitert ist. Die Hinterschiene ist schlank, wenig länger als der Schenkel und fast gerade.

Diskussion. – In Form und Skulptur der Flügeldecken stimmen alle drei Exemplare sehr gut überein. Neben den übrigen Merkmalen deutet auch dies auf eine Konspezifität der Stücke hin, da an diesem Merkmal auch die teilweise außerordentlich ähnlichen rezenten Arten anderer Gattungen der Entiminae unterschieden werden können.

Tribus Cneorhinini LACORDAIRE, 1863

Gattung *Palaeocneorhinus* n. gen.

Typus generis: *Palaeocneorhinus messelensis* n. gen. n. sp.
Derivatio nominis: παλαιός (griech.) alt, *Cneorhinus*: ähnliche rezente Gattung.

Diagnose. – Kopf: Kopf unmittelbar vor den vom Vorderrand des Halsschilds abgerückten Augen mit einer scharfen Querfurche. Rüssel etwa so lang wie breit, mit einer breiten Mittelfurche sowie über den Fühlerfurchen mit jeweils einer Seitenfurche. Kopf und Rüssel sind nach vorn konisch verengt.

Halsschild: Halsschild breiter als lang, die Oberseite besonders an den Seiten grob granuliert, die Seiten nach vorn verengt.

Flügeldecken: Flügeldecken etwa so lang wie zusammen breit, seitlich gerundet und mit regelmäßigen Punktreihen; Zwischenräume deutlich breiter als die Punkte und nicht deutlich punktiert oder granuliert.

Beziehungen. – Der breite und oben mit Furchen versehene Rüssel zeigt die Zugehörigkeit der neuen Gattung zu der Unterfamilie Entiminae. Nach der Kopfform und der Querfurche vor den Augen ist sie zu den Cneorhinini zu stellen. Eine Ähnlichkeit besteht zu einigen südafrikanischen Arten der Gattung *Protostrophus* JEKEL, 1875, die aber u.a. stärker vorstehende Augen haben, die direkt am Hinterrand des Kopfes stehen (Abb. 5c). Die südeuropäische Gattung *Attactagenus* TOURNIER, 1876 stimmt bis auf die fehlenden Seitenfurchen auf dem Rüssel gut mit der neuen Gattung überein (*Attactagenus* ist *Cneorhinus* SCHOENHERR, 1823 sehr ähnlich und wird erst in neuerer Zeit regelmäßig abgetrennt). Zum Vergleich ist der rezente *Attactagenus plumbeus* (MARSHAM, 1802) aus Frankreich abgebildet, der im Gegensatz zu anderen Arten dieser Gattung dicht beschuppt ist (Abb. 5a, 6). *Catasarcus* SCHOENHERR, 1840 aus Australien zeigt zwar Seitenfurchen auf dem Rüssel, jedoch steht die Querfurche nach vorn um mindestens einen halben Durchmesser der Augen von diesen entfernt und der Rüssel ist länger und parallelseitig oder sogar zum Ende seitlich verbreitert.

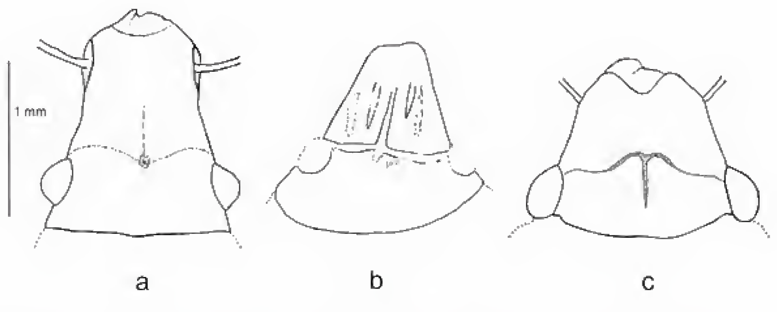

Abb. 5. Köpfe von Arten der Tribus Cneorhinini. **a**: *Attactagenus plumbeus* (MARSHAM, 1802); rezent, Frankreich (Sammlung RHEINHEIMER). **b**: *Palaeocneorhinus messelensis* n. gen. n. sp., Holotypus; Mittleres Eozän, MP11, Grube Messel; MeI 632 (FIS, Forschungsstation Grube Messel). **c**: *Protostrophus amplicollis* (FAHRAEUS, 1871); rezent, Südafrika (Sammlung RHEINHEIMER).

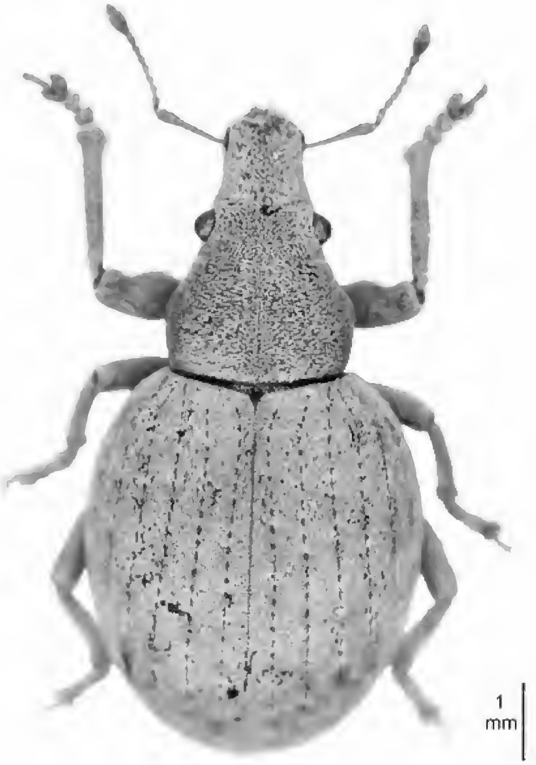

Abb. 6. *Attactagenus plumbeus* (MARSHAM, 1802); rezent, Frankreich (Sammlung RHEINHEIMER).

Palaeocneorhinus messelensis n. gen. n. sp.
Abb. 5b, 7

Holotypus: MeI 632 (Abb. 7); FIS, Forschungsstation Grube Messel.
Locus typicus: Grube Messel, Grabungsstelle 21 (M13) (Grabungsjahr 1982).
Statum typicum: Messel-Formation, Fundhorizont unbekannt.
Derivatio nominis: Benannt nach dem Fundort, der Grube Messel.

Diagnose. – Siehe Diagnose der Gattung.

Beschreibung. – Länge: 4,8 mm, in Dorsalansicht erhalten.

Integument: Das gesamte Fossil ist einfarbig schwarz. Eine Behaarung ist nicht zu erkennen.

Kopf: Die Augen sind in Dorsalansicht oval, seitlich nicht vorstehend, vom Vorderrand des Halsschilds um mehr als den halben Längsdurchmesser entfernt; die Stirn zwischen den Augen ist etwa eineinhalbmal so breit wie die Augenlänge, schwach in Längsrichtung skulptiert. Der Kopf hat unmittelbar vor den Augen eine scharfe Querfurche. Der Rüssel ist so lang wie breit, mit einer breiten Mittelfurche sowie über den Fühlerfurchen mit jeweils einer Seitenfurche. Kopf und Rüssel sind nach vorn konisch verengt. Die Fühler sind nicht sichtbar.

Halsschild: Der Halsschild erscheint weit mehr als doppelt so breit wie lang, wobei er wahrscheinlich durch die Einebnung bei der Fossilisierung verbreitert ist. Die

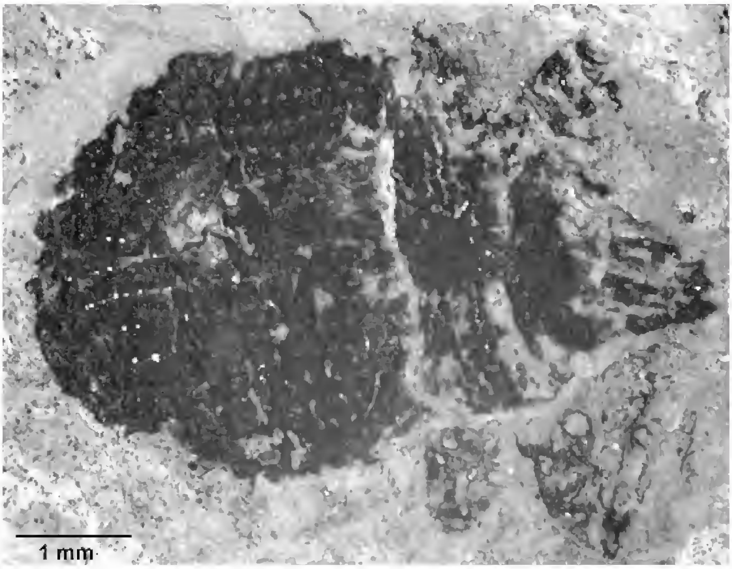

Abb. 7. *Palaeocneorhinus messelensis* n. gen. n. sp., Holotypus; Mittleres Eozän, MP11, Grube Messel; MeI 632 (FIS, Forschungsstation Grube Messel).

Oberseite ist besonders an den Seiten grob granuliert, wobei in Längsrichtung etwa 7 Tuberkeln hintereinander stehen. Die Seiten des Halsschilds sind nach vorn konvergierend.

Flügeldecken: Die Flügeldecken sind etwa so lang wie zusammen breit und seitlich gerundet. Die Proportionen können durch die Einebnung bei der Fossilisierung verändert worden sein, so dass die Flügeldecken möglicherweise etwas zu breit erscheinen. Darauf deuten etliche feine Risse hin. Oberseite mit feinen, regelmäßigen Punktreihen, von denen 8 erkennbar sind. Die Punkte stehen um den doppelten Durchmesser voneinander entfernt und die Zwischenräume sind dreimal so breit wie die Punkte und nicht deutlich punktiert oder granuliert. Das Schildchen ist nicht deutlich abgesetzt.

Beine: Die Vorder- und Mittelbeine sind rudimentär erhalten und erscheinen relativ schlank.

Tribus Anypotactini Champion, 1911

Gattung *Palaeocrassirhinus* n. gen.

Typus generis: *Palaeocrassirhinus messelensis* n. sp.
Derivatio nominis: παλαιός (griech.) alt, crassus (lat.) dick, ϱινός (griech.) Nase.

Diagnose. – Flügeldecken kräftig gereiht punktiert, mit deutlicher Schulterbeule; Halsschild vorn gerade abgeschnittenen, fast parallelseitigen, granuliert. Augen oval oder kurz oval, die Stirn dazwischen mindestens so breit wie der Rüssel; dieser etwa so lang wie breit mit seitlich gelegener Fühlerfurche; Fühlerschaft kurz.

Beziehungen. – Nach dem Bau von Rüssel und Fühlerfurchen gehört diese Gattung zu den Entiminae. Eine genaue Platzierung innerhalb der sehr zahlreichen rezenten Gattungen dieser Unterfamilie mit vielfach ungeklärten verwandtschaftlichen Beziehungen untereinander ist anhand der erhaltenen Merkmale schwierig. Der aus dem baltischen Bernstein beschriebene *Paonaupactus* Voss, 1953 zeigt einen ähnlich gebauten Kopf und vergleichbare Flügeldecken, hat aber einen etwas längeren als breiten Rüssel und der lange Fühlerschaft überragt die Augen nach hinten. Diese Gattung wurde von Kuschel (1992) in die neuweltliche Tribus Anypotactini eingeordnet und hinsichtlich ihrer verwandtschaftlichen Beziehungen diskutiert. Demnach ist die Abgrenzung von den Polydrusini u. a. durch die an der Basis freien Klauen möglich. Innerhalb der Anypotactini unterscheiden sich mehrere Gattungen wie *Hyphantus* Germar, 1824 und *Prepodellus* Kirsch, 1868 durch einen längeren und schlankeren Rüssel. *Hyphantus* hat außerdem einen in Längsrichtung stark gewölbten Halsschild. Vorläufig wird die neue Gattung in die Nähe von *Paonaupactus* gestellt.

Beschreibung. – Kopf: Die rundlichen bis ovalen Augen sind um fast einen Durchmesser vom Vorderrand des Halsschilds entfernt, die Stirn zwischen den Augen ist fast so breit wie der Rüssel, dieser ist in dorsaler Ansicht parallelseitig, etwas breiter als lang. Der Fühlerschaft ist nur teilweise erhalten, kurz.

Halsschild: Der Halsschild ist etwas kürzer als der Kopf einschließlich Rüssel. Die Vorderhüften stehen etwa in der Mitte zwischen Vorder- und Hinterrand des Halsschilds. Die Vorderränder der Flügeldecken sind konvex vorgezogen, so dass die Halsschildbasis doppelbuchtig erscheint.

Flügeldecken: Die Flügeldecken sind in Längsrichtung gleichmäßig gewölbt, mit kräftigen, regelmäßigen Punktreihen. Das Schildchen ist dreieckig.

Beine: Die Schenkel sind relativ schlank, hinter der Mitte erweitert, nicht gezähnt. Die Vorderschienen etwa so lang wie die Schenkel, am Ende mit einem nach innen gerichteten Dorn.

Palaeocrassirhinus rugosithorax n. gen. n. sp.
Abb. 8

Holotypus: MeI 3598 (Abb. 8); FIS, Forschungsstation Grube Messel.
Locus typicus: Grube Messel, Grabungsstelle H8 (Grabungsjahr 1991).
Stratum typicum: Messel-Formation, Fundbereich 0,27–0,53 m über Leithorizont α.
Derivatio nominis: rugosus (lat.) runzelig, θώραξ (griech.) Brustkorb (Halsschild).

Diagnose. – Flügeldecken kräftig gereiht punktiert mit deutlicher Schulterbeule; Halsschild vorn gerade abgeschnittenen, granuliert und beschuppt, im Gegensatz zu *P. messelensis* n. gen. n. sp. in Seitenansicht ohne erkennbare Querfurche hinter dem Vorderrand; Rüssel sehr kurz und breit mit seitlich gelegener Fühlerfurche sowie einem kurzen Fühlerschaft, der die länglich ovalen Augen nicht erreicht.

Beschreibung. – Länge: 3,8 mm, in Lateralansicht erhalten.

Integument: Das gesamte Fossil ist einfarbig schwarz. Eine Behaarung ist nicht zu beobachten. An den Seiten des Halsschilds sind einzelne etwas keilförmige Schuppen zu erkennen. Die rauhe, rundliche Skulptur der Flügeldecken ist besonders auf

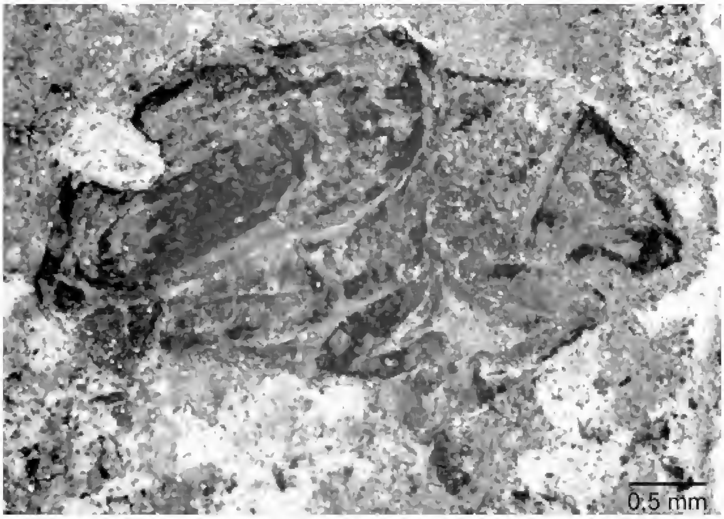

Abb. 8. *Palaeocrassirhinus rugosithorax* n. gen. n. sp., Holotypus; Mittleres Eozän, MP11, Grube Messel; MeI 3598 (FIS, Forschungsstation Grube Messel).

dem vorderen und hinteren Drittel zu erkennen und deutet auf eine dichte, anliegende Beschuppung hin.

Kopf: Die Augen sind länglich oval, um einen Durchmesser vom Vorderrand des Halsschilds entfernt, dem Oberrand des Kopfes viel näher als dem Unterrand. Der Rüssel ist breit, etwas kürzer als der Kopf, von dem er nicht abgesetzt ist. Der Fühlerschaft ist kurz, und erreicht die Augen nicht; die Fühlerfurche seitlich vor den Augen ist zum Unterrand des Rüssels gerichtet.

Halsschild: Der Halsschild so lang wie der Kopf einschließlich Rüssel, die Oberseite grob granuliert-punktiert. Der Vorderrand ist hinter den Augen gerade abgeschnitten ohne Augenlappen und ohne laterale Einschnürung. In Seitenansicht ist die Oberseite fast gerade.

Flügeldecken: Flügeldecken sind dreimal so lang wie der Halsschild, mit kräftigen, an den Seiten verwaschenen Punktreihen, von denen 8 erkennbar sind. Die Punktreihen sind etwa so breit wie die Zwischenräume, die kräftigen Punkte der äußeren Reihe sind um etwa einen Durchmesser voneinander entfernt. In Seitenansicht überragen die Flügeldecken an der Basis den Halsschild deutlich nach oben.

Beine: Die Beine sind schlank, die Schenkel ungezähnt, die Schienen zum Ende erweitert. Ein Vorderfuß ist deutlich erkennbar und etwa so breit wie die Mittelschienen. Das Klauenglied erscheint in Aufsicht, und die Klauen sind deshalb nur schwach abgesetzt, wahrscheinlich an der Basis getrennt.

Palaeocrassirhinus messelensis n. gen. n. sp.
Abb. 9–10

Holotypus: MeI 5302 (Abb. 9); FIS, Forschungsstation Grube Messel.
Locus typicus: Grube Messel, Grabungsstelle E8/9 (Grabungsjahr 1996)
Stratum typicum: Messel-Formation, Fundbereich 0,52–0,82 m unter Leithorizont α.

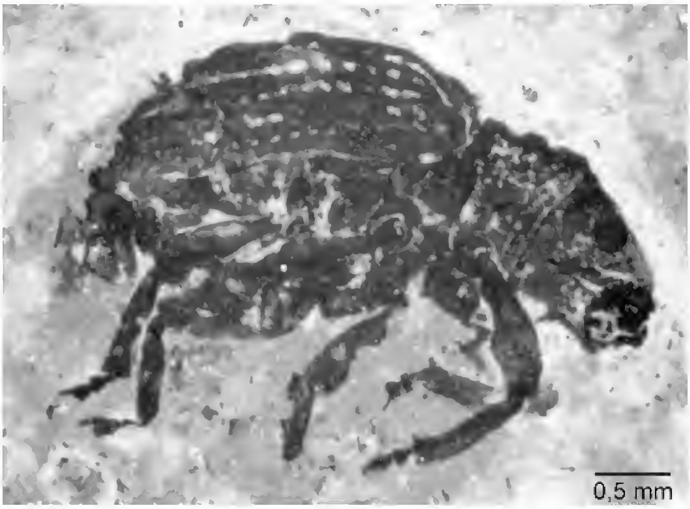

Abb. 9. *Palaeocrassirhinus messelensis* n. gen. n. sp., Holotypus; Mittleres Eozän, MP11, Grube Messel; MeI 5302 (FIS, Forschungsstation Grube Messel).

Paratypus: MeI 3358 (Abb. 10, Fundort: Grube Messel, Grabungsstelle E11 (Grabungsjahr 1990), Fundbereich: 4,10–4,50 m unter Leithorizont α.

Derivatio nominis: Benannt nach dem Fundort, der Grube Messel.

Diagnose. – Flügeldecken kräftig gereiht punktiert, mit deutlicher Schulterbeule; Halsschild vorn gerade abgeschnittenen, granuliert und beschuppt, im Gegensatz zu *P. rugosithorax* n. gen. n. sp. mit in Seitenansicht erkennbarer Querfurche hinter dem Vorderrand, die bis auf die Unterseite deutlich bleibt. Augen kürzer oval als bei der vorigen Spezies; Rüssel kurz und breit mit seitlich gelegener Fühlerfurche; Halsschild an der seitlichen Vorderkante ohne Borsten oder Borstenpunkte.

Beziehungen. – Zwar ist nicht erkennbar, ob die Klauen an der Basis getrennt sind, trotzdem ermöglichen die übrigen Merkmale und die Ähnlichkeit mit der vorigen Art die Zuordnung zur Gattung *Palaeocrassirhinus* n. gen.

Beschreibung. – Holotypus (Abb. 9): Länge: 3,3 mm, in Lateralansicht erhalten.

Integument: Das gesamte Fossil ist einfarbig schwarz. Eine Behaarung ist nicht zu beobachten.

Kopf: Die Augen sind kurz oval, rundlicher als bei der vorigen Art, um fast einen Durchmesser vom Vorderrand des Halsschilds entfernt. Der Rüssel ist etwas breiter als lang, der Fühlerschaft ist nur teilweise erhalten.

Halsschild: Der Halsschild ist etwas kürzer als der Kopf einschließlich Rüssel, grob etwas verrunzelt granuliert, die Oberseite gerade. Einen halben Augendurchmesser hinter dem Vorderrand befindet sich eine gerade, feine Furche, die von den Seiten nach unten verläuft und vorn von den zusammenstehenden Vorderhüften schmal getrennt bleibt. Die Vorderhüften stehen etwa in der Mitte zwischen Vorder- und Hinterrand des Halsschilds.

Flügeldecken: Die Flügeldecken sind in Längsrichtung gleichmäßig gewölbt, mit kräftigen, regelmäßigen Punktreihen, von denen 5 erkennbar sind. Die Punkte ste-

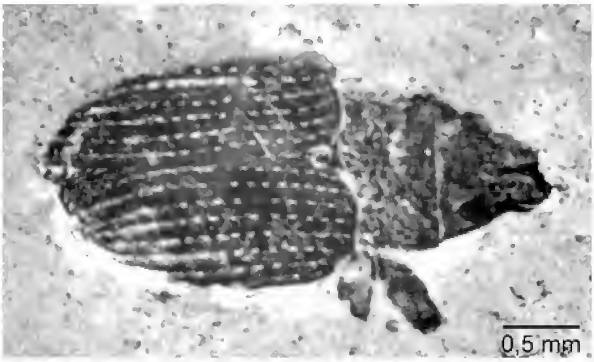

Abb. 10. *Palaeocrassirhinus messelensis* n. gen. n. sp., Paratypus; Mittleres Eozän, MP11, Grube Messel; MeI 3358 (FIS, Forschungsstation Grube Messel).

hen um eineinhalb Durchmesser voneinander entfernt und die Zwischenräume sind doppelt so breit wie die länglichen Punkte und erscheinen glatt.

Beine: Die Schenkel sind relativ schlank, hinter der Mitte erweitert, nicht gezähnt. Die Vorderschienen sind etwa so lang wie die Schenkel, die Außenseite ist fast gerade, vorn leicht nach innen gebogen: Die Innenseite ist ganz leicht doppelbuchtig, am Ende ebenfalls nach innen gebogen und trägt einen nach innen gerichteten Dorn.

Paratypus (Abb. 10): Länge: 2,9 mm, in Dorsalansicht erhalten.

Der Paratypus entspricht in den Merkmalen von Integument, Kopf, Halsschild und Flügeldecken dieser Gattung und ist wegen der kurz ovalen Augen dieser Art zuzurechnen. Die Seitenfurche des Halsschilds ist in dieser Ansicht nicht sichtbar.

Kopf: Der Kopf ist nach vorn gerundet verengt. Die Augen sind rundlich, seitlich ein wenig aus der Kopfwölbung vorstehend, um fast einen Durchmesser vom Vorderrand des Halsschilds entfernt. Die Stirn zwischen den Augen ist fast so breit wie der Rüssel, fein punktiert. Der Rüssel ist etwas breiter als lang, fast parallelseitig und mit einer Mittelfurche, die die Augenmitte erreicht. Die Fühler sind nicht sichtbar.

Halsschild: Der Halsschild ist eineindrittelmal so breit wie in der Mitte lang, etwas kürzer als der Kopf einschließlich Rüssel und fast parallelseitig. Die Oberseite ist grob etwas verrunzelt granuliert, wobei in Längsrichtung etwa 6–7 Tuberkeln hintereinander stehen. Die Vorderränder der Flügeldecken sind konvex vorgezogen, so dass die Halsschildbasis doppelbuchtig erscheint.

Flügeldecken: Die Flügeldecken sind eineindrittelmal so lang wie an der Basis zusammen breit, kurz hinter der Basis eineinviertelmal so breit wie der Halsschild, von der Basis an leicht und im letzten Viertel stark gerundet verengt, mit kräftigen, regelmäßigen Punktreihen, von denen 8 erkennbar sind. Die Punkte stehen um eineinhalb Durchmesser voneinander entfernt und die Zwischenräume sind doppelt so breit wie die länglichen Punkte und erscheinen glatt. Das Schildchen ist dreieckig.

Beine: Die Vorder- und Mittelschenkel sind rudimentär erhalten und erscheinen relativ schlank.

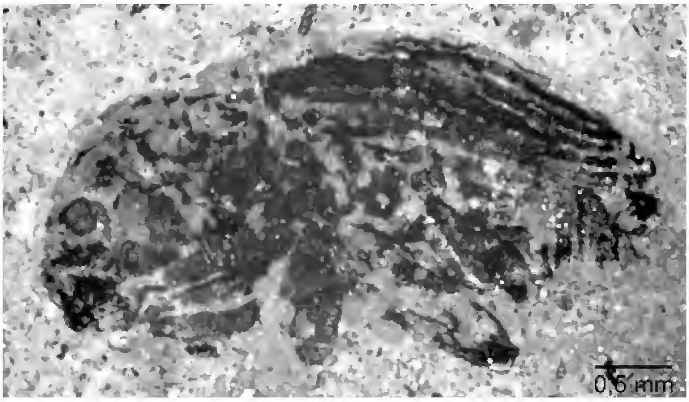

Abb. 11. *Palaeocrassirhinus* cf. *messelensis* n. gen. n. sp.; Mittleres Eozän, MP11, Grube Messel; MeI 3682 (FIS, Forschungsstation Grube Messel).

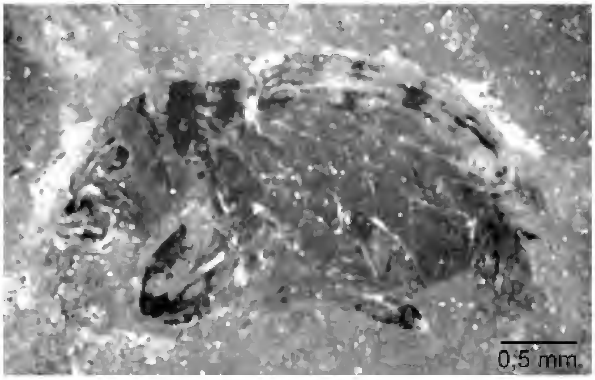

Abb. 12. *Palaeocrassirhinus* cf. *messelensis* n. gen. n. sp.; Mittleres Eozän, MP11, Grube Messel; MeI 4727 (FIS, Forschungsstation Grube Messel).

Palaeocrassirhinus cf. *messelensis* n. gen. n. sp.
Abb. 11–12

Material: MeI 3682; Fundort: Grube Messel, Grabungsstelle F11 (Grabungsjahr 1991), Fundbereich: 4,16–4,46 m über Leithorizont α. MeI 4727; Fundort: Grube Messel, Grabungsstelle E9 (Grabungsjahr 1994), Fundbereich: 0,24–0,44 m unter Leithorizont α.

Das in Seitenansicht schräg von unten erhaltene Fossil MeI 3682 (Länge: 3,5 mm, Abb. 11) zeigt wenig feine Details in einer von den anderen Stücken abweichenden Projektion und wird deshalb nicht als Paratypus betrachtet. Bei ihm sind die Hinterleibs-Segmente 3 und 4 zusammen so lang wie Segment 5.

MeI 4727 (Länge: 3,0 mm, Abb. 12) ist ebenfalls in Seitenansicht erhalten und weicht durch die lochartigen Fühlerfurchen ab. In dieser Hinsicht erinnert das Exemplar etwas an Gattungen wie *Pseudomyllocerus* Desbrochers, 1872. Allerdings könnte es sich auch um eine Verformung bei der Fossilisierung handeln, da der Habitus ansonsten mit MeI 3682 übereinstimmt. Auch dieser Fund wird wegen der etwas abweichenden Merkmale am Rüssel nicht als Paratypus klassifiziert.

MeI 3682 und MeI 4727 werden vorläufig zu *Palaeocrassirhinus messelensis* n. gen. n. sp. gerechnet. Weitere Funde wären erforderlich, um diese Zuordnung abzusichern.

3.2. Funde aus dem Baltischen Bernstein

Unterfamilie Curculioninae Latreille, 1802
Tribus Derelomini Lacordaire, 1866

Gattung *Protoceletes* n. gen.

Typus generis: *Protoceletes wolfschwenningerae* n. gen. n. sp.
Derivatio nominis: πϱοτού (griech.) vor, *Celetes*: ähnliche rezente Gattung.

Diagnose. – Kopf breiter als lang, Augen rundlich, seitlich aus der Wölbung des Kopfes etwas vorstehend; Rüssel schlank, parallelseitig, gebogen; Glied 1 der 7-gliedrigen Fühlergeißel länger als die folgenden, diese etwa gleich lang und viel länger als breit; Fühlerkeule spindelförmig, aus drei durch eine deutliche Naht voneinander getrennten Segmenten bestehend, von denen das erste kürzer ist als die folgenden zusammen. Flügeldecken mit feinen Punktreihen. Der an der Basis parallelseitige Halsschild ist nach vorn gerundet verschmälert. Naht zwischen Sternit 1 und 2 in der Mitte undeutlich, beide etwa gleich lang, Sternit 2 so lang wie 3 und 4 zusammen. Alle Schenkel breit und scharf stumpfwinklig gezähnt, die Vorderschienen innen doppelbuchtig, Schienen am Ende an der Innenseite mit einem feinen, nach innen gerichteten Dorn („mucro“ nach der Nomenklatur von Marshall 1932).

Beziehungen. – *Protoceletes* n. gen. stimmt mit dem weltweit verbreiteten *Derelomus* Schoenherr, 1825 in dem breiten Kopf mit seitlich vorstehenden Augen und der Form der Fühlerkeule überein, von dem sie aber durch die gezähnten Schenkel und die schlanke Fühlergeißel abweicht. Ähnlich sind auch die neotropischen *Celetes* Schoenherr, 1836 und *Phytotribus* Schoenherr, 1843, die am Ende der Schienen keinen deutlichen Dorn tragen und bei denen die meist etwas ovalen Augen seitlich nicht aus der Wölbung des Kopfes hervorragen. Bei *Celetes* ist der Halsschild auch zur Basis meist deutlich gerundet verengt und das erste Glied der Fühlerkeule ist konisch und länger als die folgenden zusammen. Bei *Phytotribus* sind die Flügeldecken stärker gewölbt. Kuschel (1952) gibt einen Bestimmungsschlüssel für die meisten verwandten südamerikanischen Gattungen an.

Protoceletes wolfschwenningerae n. gen. n. sp.
Abb. 13

Holotypus: BB-593-K (SMNS, Bernsteinsammlung).
Derivatio nominis: Benannt zu Ehren von Frau Dr. K. Wolf-Schwenninger, die bei der Bearbeitung des Bernsteinmaterials aus dem Staatlichen Museum für Naturkunde Stuttgart wertvolle Hilfe leistete.

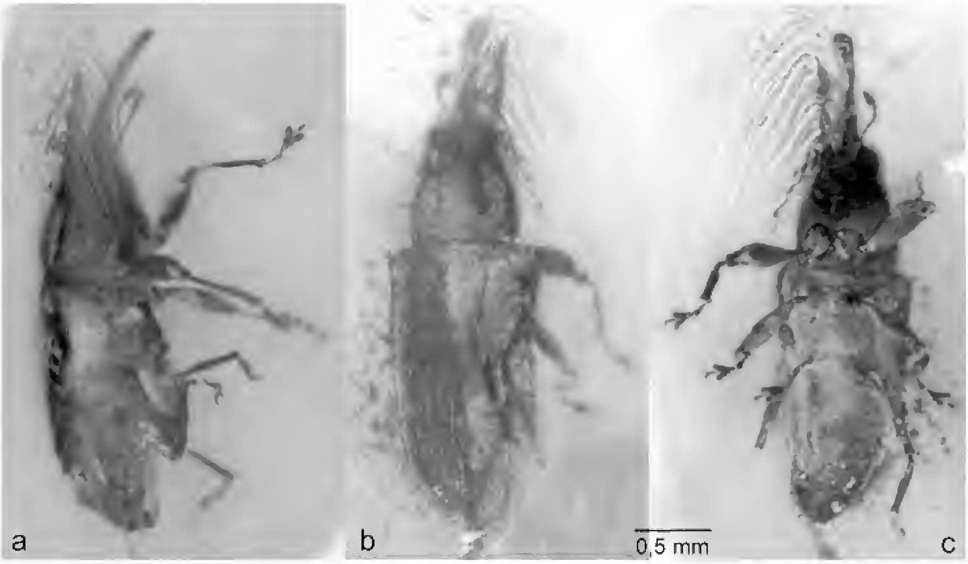

Abb. 13. *Protoceletes wolfschwenningerae* n. gen. n. sp., Holotypus; Eozän, Baltischer Bernstein. **a**: lateral; **b**: dorsal; **c**: ventral; BB-593-K (SMNS, Bernsteinsammlung).

Diagnose. – Siehe Diagnose der Gattung.

Beschreibung. – Länge: 2,6 mm; die rechte Flügeldecke ist beschädigt, möglicherweise immatur, da etwas durchscheinend und leicht verformt und deshalb wahrscheinlich erst schwach chitinisiert.

Integument: Das gesamte Fossil ist einfarbig rotbraun, die Körperanhänge und der Kopf etwas dunkler. Die Flügeldecken sind schwer erkennbar ziemlich dicht mit hellen und dunklen anliegenden Schuppenhaaren bekleidet, die Unterseite teilweise mit einem dichten, hellen, nur bei bestimmtem Lichteinfall erkennbaren Schuppenkleid.

Kopf: Der Kopf ist breiter als lang, die Stirn zwischen den Augen breiter als der Rüssel. Die Augen sind rundlich, seitlich aus der Wölbung des Kopfes etwas vorstehend. Der Rüssel ist so lang wie Kopf und Halsschild zusammen, fast parallelseitig und gleichmäßig wenig gebogen, die Fühlereinlenkung liegt etwa in der Mitte. Der Fühlerschaft ist lang und erreicht die Augen. Glied 1 der 7-gliedrigen Fühlergeißel ist länger als die folgenden, diese sind etwa gleich lang und viel länger als breit. Die Fühlerkeule ist spindelförmig und besteht aus drei durch eine deutliche Naht voneinander getrennten Segmenten, von denen das erste kürzer ist als die folgenden zusammen.

Halsschild: Der Halsschild ist ein wenig breiter als lang, die Oberseite ist fein, wenig dicht und etwas ungleichmäßig punktiert. Er ist an der Basis parallelseitig und nach vorn schwach gerundet verengt. Vorderhüften stoßen zusammen, sind vom Vorderrand des Halsschildes um mehr als einen Durchmesser entfernt und dem Hinterrand viel mehr genähert. In Seitenansicht ist die Oberseite gerade.

Flügeldecken und Abdomen: Die Flügeldecken sind parallelseitig, deutlich breiter und gut doppelt so lang wie der Halsschild, fast doppelt so lang wie zusammen breit, mit sehr feinen Punktstreifen, deren Zwischenräume mehr als dreimal so breit sind wie die Streifen. Die Naht zwischen Sternit 1 und 2 ist in der Mitte undeutlich, beide sind etwa gleich lang. Sternit 2 ist so lang wie 3 und 4 zusammen und etwas länger als Sternit 5.

Beine: Die Schenkel sind keulenförmig, breit und scharf stumpfwinklig gezähnt, besonders die Vorderschienen innen doppelbuchtig, am Ende innen mit einem nach innen gerichteten Dorn. Glied 1 der Tarsen ist schlank, länger als die Schienen breit, die beiden folgenden sind von abnehmender Länge und zunehmend breiter. Glied 3 ist breiter als die Schienen an der breitesten Stelle und tief gelappt. Das Klauenglied überragt Glied 3 um dessen Länge und trägt lange, schlanke, einfache Klauen.

Unterfamilie Molytinae Schoenherr, 1823

Gattung *Electrotribus* Hustache, 1942

Typus generis: *Electrotribus theryi* Hustache, 1942

Diagnose (nach Hustache 1942, erweitert). – Die bisher bekannten Arten sind dicht und grob beschuppt. Kopf halbkugelig, die quer ovalen, seitenständigen Augen nicht aus der Wölbung vorstehend. Rüssel an der Basis im Querschnitt rund, kaum breiter als die Schienen, fast gerade oder deutlich gebogen, mindestens so lang wie der Halsschild, die Oberseite bis vorn kräftig punktiert. Die Fühler in der Mitte des Rüssels oder davor eingelenkt, der lange, schlanke Schaft die Augen nicht ganz erreichend. Halsschild an den Seiten ohne Augenlappen, in Dorsalansicht kurz vor der Basis am breitesten und nach vorn gerundet verengt. Vorderbrust einfach, ohne Kiele, Vorderhüften zusammenstehend, mindestens um ihren Durchmesser vom Vorderrand der Vorderbrust abgerückt, dem Hinterrand viel stärker genähert. Schildchen sichtbar, Schultern deutlich, Flügeldecken in der vorderen Hälfte fast parallelseitig, ein wenig breiter als der Halsschild, Naht zwischen Sternit 1 und 2 in der Mitte fast erloschen, viel schwächer als zwischen den übrigen Sterniten. Die Schienen tragen am Ende einen kräftigen, nach innen gerichteten Dornfortsatz, der nicht am Innenrand, sondern etwas davon abgerückt entspringt und nach der Nomenklatur von Marshall (1932) einem „uncus“ entspricht. Über diesem Dorn befindet sich an der Innenseite der Schienen ein Borstenbüschel.

Beziehungen. – Bisher wurde *Electrotribus* zu den Curculioninae, Tribus Derelomini gestellt (Alonso-Zarazaga & Lyal 1999). Kuschel (1992) stellte zuvor die Gattung zu den Curculionini und diskutierte ihre Merkmale im Vergleich zu *Celetes* Schoenherr, 1836 (Derelomini). Nach der Bildung der Schienen gehört diese Gattung jedoch zu den Molytinae (sensu Alonso-Zarazaga & Lyal 1999). Die Form des an der Basis wenig verengten Halsschilds mit den vom Vorderrand abgerückten Hüften, der runde, mäßig gebogene Rüssel mit lateralen Fühlerfurchen und langem Fühlerschaft, deutliche Schultern, ein sichtbares Schildchen und die rauhe Skulptur der Oberseite stimmen mit den Pissodini überein. Bei diesen sind jedoch die Vorderhüften getrennt und die Schienen sind am Ende anders gebildet. Hier geht bei den Pissodini der „uncus“ ganz vom Außenrand der Schienen aus und innen befindet sich ein zusätzlicher nach innen gerichteter Dorn („mucro“ nach Marshall

1932). Außerdem sind besonders am Apex der Hinterschienen meist deutliche Borstenreihen erkennbar. Es ist möglich, dass es sich bei dieser Gattung um Vorfahren der Pissodini handelt, die hinsichtlich der Schienen-Bildung höher differenziert erscheinen. Eine sichere Zuordnung zu einer rezenten Tribus ermöglichen die äußeren Merkmale nicht, so dass sie vorläufig in die Unterfamilie Molytinae, Tribus incertae sedis gestellt wird. Eine Verwandtschaft mit den Pissodini ist wahrscheinlich.

Die Form des „uncus" und der Halsschildunterseite ähnelt *Thalasselephas* EGOROV & KOROTYAEV, 1976 (Thalasselephantini), jedoch ist bei dieser in Ostasien und Nordamerika verbreiteten Gattung das Schildchen nicht sichtbar, und die Schultern sind verrundet. Dabei könnte es sich um eine Anpassung an ein Leben in der Bodenstreu mit Verlust der Flugfähigkeit handeln. Auch die Thalasselephantini stehen demnach in näherer Beziehung zu der neuen Tribus. Um zu klären, welches dieser beiden rezenten Taxa näher mit dem neuen Taxon verwandt ist, wäre weiteres fossiles Material sehr nützlich.

Außerdem bestehen Ähnlichkeiten mit den Phrynixini und Anchonini, bei denen u.a. die Schultern verrundet und das Schildchen nicht sichtbar sind.

Electrotribus erectosquamata n. sp.
Abb. 14

Holotypus: BB-1458-K (SMNS, Bernsteinsammlung)
Paratypen: 6 Exemplare (C-004–C-009), Sammlung RHEINHEIMER.
Derivatio nominis: erectus (lat.) aufrecht, squamatus (lat.) beschuppt.

Diagnose. – Kopf halbkugelig, die quer ovalen Augen nicht aus der Wölbung vorstehend. Der Rüssel ist in der vorderen Hälfte deutlich gebogen, kaum länger als der Halsschild, in Seitenansicht vor der Fühlereinlenkung kräftig verjüngt, die Oberseite bis zum Ende grob längsrunzlig punktiert, fast gerade in den Kopf übergehend. Die Fühler deutlich vor der Mitte des Rüssels eingelenkt, der lange, schlanke Schaft die Augen nicht ganz erreichend. Flügeldecken knapp eineinhalbmal so lang wie zusammen breit, in der basalen Hälfte seitlich fast parallelseitig, ein wenig breiter als der Halsschild, letzterer kurz vor der Basis am breitesten und nach vorn gerundet verengt, deutlich breiter als lang. Halsschild und Flügeldecken mit groben Schuppen dicht bedeckt, Schenkel ungezähnt.

Beschreibung. – Länge: 3,5 mm.

Integument: Das Fossil ist schwarz, Halsschild, Flügeldecken, Beine und der Kopf sind bis zur Fühlereinlenkung dicht mit anliegenden, groben Schuppen bedeckt. Dazwischen befinden sich überall zum Ende erweiterte, dicke Schuppen, die manchmal gebogen sind und auf den Flügeldecken einreihig auf den Zwischenräumen fast senkrecht abstehen.

Kopf: Die Augen sind quer, seitenständig, nicht aus der Wölbung des Kopfes vorstehend, in Seitenansicht breiter als der Rüssel an der Basis. Der Kopf ist halbkugelig, dicht punktiert, die Stirn zwischen den Augen so breit wie der Rüssel an der Spitze. Der Rüssel ist ein wenig länger als der Halsschild, in Dorsalansicht von der Basis zum Ende gleichmäßig etwas verschmälert, in Seitenansicht bis zur Fühlereinlenkung vor der Mitte fast gerade und von gleicher Höhe, davor kräftig gebogen und zum Ende auf die halbe Breite verjüngt. Der Fühlerschaft ist lang, schlank, am Ende keulenförmig und leicht abgewinkelt, die Augen fast erreichend. Glied 1 der 7-glie-

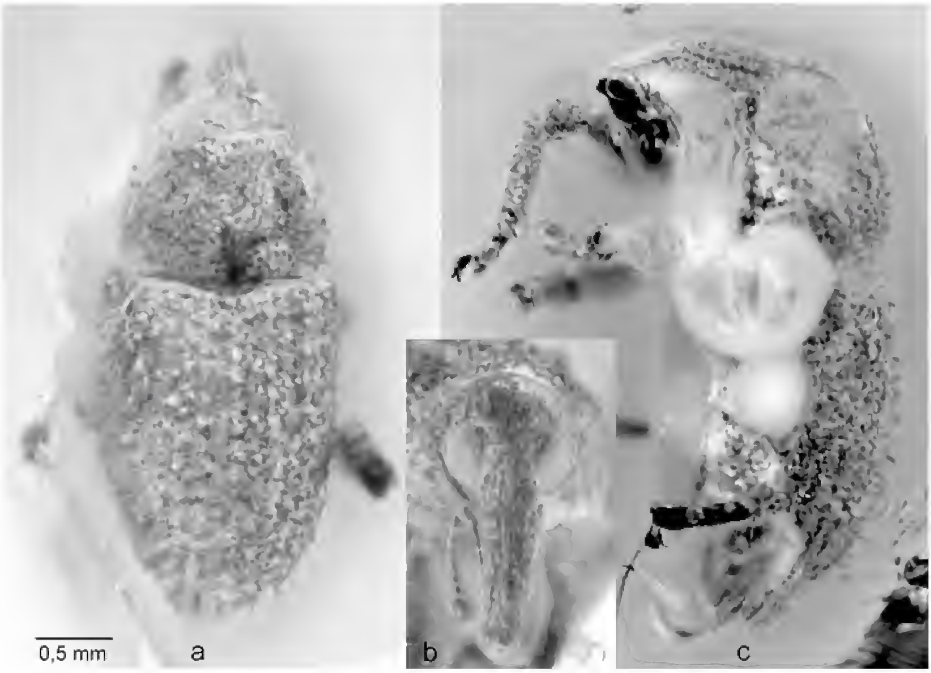

Abb. 14. *Electrotribus erectosquamata* n. sp., Holotypus; Eozän, Baltischer Bernstein. **a**: Körper dorsal; **b**: Kopf frontal; **c**: Körper lateral; BB-1458-K (SMNS, Bernsteinsammlung).

drigen Fühlergeißel ist länger und breiter als das folgende, Glied 2 ist mehr als eineinhalbmal so lang wie breit, die übrigen sind viel kürzer und zunehmend breiter, mit langen, abstehenden Borsten. Die Keule ist viel breiter als die Geißel.

Halsschild: Der Halsschild ist ein Drittel breiter als lang, kurz vor der Basis am breitesten, nach vorn gerundet verengt, an der Basis doppelbuchtig. Soweit durch die dichte Beschuppung erkennbar ist die Oberseite dicht und ziemlich grob punktiert. Vorderhüften sind zusammenstehend, etwa um ihren Durchmesser vom Vorderrand der Vorderbrust entfernt und ohne Kiele. In Seitenansicht ist die Oberseite leicht gewölbt.

Flügeldecken und Abdomen: Die Flügeldecken sind bis zur Mitte parallelseitig, dahinter bis zum Ende gleichmäßig gerundet verengt. Sie sind etwas breiter und gut doppelt so lang wie der Halsschild und knapp eineinhalbmal so lang wie zusammen breit. Soweit durch die grobe Beschuppung erkennbar tragen sie kräftige Punktstreifen. Der 5. Zwischenraum ist an der Basis etwas verbreitert und ein wenig stärker gewölbt vorstehend als die benachbarten. Die Schultern sind deutlich, die Basis ist doppelbuchtig. Bei einem Paratypus (C-004) ist Sternit 1 etwas länger als Sternit 2, die Naht zwischen beiden ist in der Mitte deutlich. Sternit 3 und 4 sind viel kürzer, gleich lang, zusammen etwa so lang wie Sternit 5.

Beine: Die Schenkel sind in der Mitte so breit wie der größte Augendurchmesser und ein Viertel kürzer als der Halschild. Sie sind ungezähnt, besonders die Vorderschienen sind innen doppelbuchtig, und tragen am Ende einen kräftigen, nach innen gerichteten Dornfortsatz, der nicht am Innenrand, sondern etwas davon abgerückt entspringt. Über diesem Dorn steht an der Innenseite der Schienen ein langes Borstenbüschel. Borstenreihen sind am Ende der Schienen nicht erkennbar. Die Tarsen sind dicht mit Borsten bekleidet. Glied 1 der Tarsen ist schlank, Glied 2 kürzer und breiter, Glied 3 ist so breit wie die Schienen an der breitesten Stelle und tief gelappt. Das Klauenglied überragt Glied 3 um etwas weniger als dessen Länge, mit langen, schlanken, einfachen Klauen.

Beziehungen. – Von *E. weigangae* (ULKE, 1947), von dem mir mehrere Exemplare vorlagen (z.B. BB-1657-K und BB-1240-K; SMNS, Bernsteinsammlung) und *E. theryi* HUSTACHE, 1942 unterscheidet sich die neue Art durch den kürzeren, viel stärker gebogenen, gröber skulptierten, bis zur Fühlereinlenkung dicht beschuppten und in Seitenansicht vorn verjüngten Rüssel. Außerdem sind die Flügeldecken viel kürzer (bei *weigangae* doppelt so lang wie zusammen breit), der Halsschild ausgeprägter breiter als lang und die Schenkel ungezähnt. Möglicherweise erfordern diese Unterschiede eine eigene Gattung, jedoch ist dafür das Auffinden von weiterem fossilen Material erforderlich.

4. Diskussion

Die Unterfamilie Entiminae (ALONSO-ZARAZAGA & LYAL 1999) ist auch heute in der Paläarktis und weltweit mit über 10000 beschriebenen Arten reich vertreten. Die Verbreitung erstreckt sich von den Niederungen bis zur Grenze des Pflanzenwuchses im Hochgebirge, vom feucht-gemäßigten Bereich bis in die Wüsten Mittelasiens und Australiens und von den Tropen bis jenseits der Polarkreise.

Soweit bekannt leben die Larven ganz überwiegend im Boden und ernähren sich von Wurzeln. Die Imagines sind meistens oligo- oder polyphag an zweikeimblättrigen Kräutern, Sträuchern oder Bäumen, einkeimblättrige Pflanzen werden gemieden. Vergleichsweise wenige finden sich ausschließlich auf Koniferen. Es gibt sowohl flugfähige als auch nicht flugfähige Arten, wobei letztere – wie bei anderen Tiergruppen auch – im Hochgebirge, auf Inseln und in den Wüsten zunehmen.

Insgesamt sind die Entiminae, von Ausnahmen abgesehen, in ihrem Habitus recht homogen. Eine Aufsammlung aus den Tropen ist nicht unbedingt auf den ersten Blick von Tieren aus dem gemäßigten Bereich zu unterscheiden, und Exemplare aus einer Wüste fallen lediglich durch die oftmals hell-bräunliche Farbe auf, eine Anpassung an die sandfarbene Umgebung. Auch die Zusammensetzung dieser Kollektive kann hinsichtlich der darin enthaltenen Tribus und Gattungen durchaus ähnlich sein. Allerdings führen lokale Schwerpunkte in der Differenzierung manchmal zu einem bemerkenswerten Artenreichtum einzelner Gattungen in den jeweiligen Gebieten. So sind etwa 160 *Protostrophus*-Arten aus Südafrika und den angrenzenden Ländern beschrieben. Sie stellen damit über 80% der Cneorhinini in dieser Region.

Die Funde aus Messel gehören zu auch heute noch verbreiteten Tribus und zeigen keine auffällig abweichenden Merkmale. Offenbar waren bereits vor ca. 50 Millionen Jahren viele heute bekannte Rüsselkäfer-Tribus und -Gattungen vorhanden. Darauf deutet auch die nicht publizierte eigene Untersuchung von über hundert Arten aus dem Baltischen Bernstein hin, von denen bisher nur etwa 20 beschrieben sind (KUSCHEL 1992). Die Anfänge dieser Familie gehen mindestens bis ins Mesozoikum zurück (ARNOLDI et al. 1977). Die aus dieser Zeit bekannten, ursprünglichen orthognathen Gattungen unterscheiden sich jedoch von der Tertiär-Fauna erheblich.

Wie die Bernstein-Fossilien weisen auch die Funde aus Messel darauf hin, dass die Aufspaltung in die heutigen Unterfamilien und Tribus deutlich vor dem Eozän erfolgt ist. Seit dieser Zeit erscheinen die morphologischen Veränderungen begrenzt. Das hohe Alter der Rüsselkäfer-Taxa zeigt sich auch in einer großen genetischen Variationsbreite, die die molekulare Klassifikation erschwert (WINK et al. 1997).

Die Umgebung des Messel-Sees dürfte vielfältige Lebensräume für Entiminae geboten haben. Vermutlich haben sich die Larven in etwas höher gelegenen Bereichen entwickelt, da dauerhaft staunasser Boden für sie weniger geeignet ist. Die Imagines sind überwiegend sehr beweglich und überwinden fliegend oder laufend gewisse Entfernungen. Sie könnten von überhängenden Ästen in den See gefallen sein. Heute kann man z. B. an Gewässerrändern etliche *Polydrusus*- und *Phyllobius*-Arten von Laubbäumen klopfen. Sie können aber auch bei Regenfällen mitgerissen worden sein. Im Anspülicht unserer Flüsse ist besonders bei Hochwasser eine große Zahl von Insekten zu beobachten, darunter auch Entiminae.

In Messel finden sich Pflanzenfamilien, die heute nur in den Tropen vorkommen (z. B. Pandanaceae) und dort zum Teil nur noch ein begrenztes Vorkommen haben (z. B. Mastixiaceae in Südostasien). Diese Florenelemente weisen auf ein feuchtwarmes Klima hin. Andererseits wurde auch Pollen von Fagaceae gefunden, die zwar rezent weltweit vorkommen, aber eher etwas gemäßigtere, trockenere und kühlere Lebensräume bevorzugen. Offenbar standen sie etwas vom See entfernt, da die charakteristischen Früchte dort nicht gefunden wurden (SCHAAL & ZIEGLER 1992). Es ist also anzunehmen, dass in der Umgebung des Sees durchaus unterschiedliche Lebensräume vorhanden waren, die auch etwas trockenere und kühlere Elemente enthielten.

Die hier beschriebenen Arten von Messel können im Einzelnen wie folgt ökologisch interpretiert werden:

Die Tribus Otiorhynchini ist heute vorwiegend paläarktisch über Europa und Nordafrika bis nach Zentralasien verbreitet. *Otiorhynchus* ist bei weitem die artenreichste Gattung, es gibt aber darüber hinaus einzelne Gattungen in fast allen Teilen der Welt, z. B. *Sciobius* in Südafrika. Dabei werden sowohl Steppenbiotope als auch Wälder besiedelt, die in gemäßigten, mediterranen und ariden Gebieten liegen. Tropische Arten sind bisher nicht bekannt. Etliche rezente Arten kommen in Buchen- und Eichenwäldern vor, andere bevorzugen eine offenere Vegetation. Eventuell könnten Bestände mit Fagaceae oder mit Gebüsch bewachsene Areale als fossiler Lebensraum in Betracht kommen.

Die Tribus Cneorhinini bevorzugt heute mediterrane Busch- oder Steppenvegetation. Es gibt auch Vertreter in gemäßigten und tropischen Gebieten. Wenn die heutige Situation auf das Eozän übertragbar ist, könnte die fossile Art möglicherweise in einer offenen Buschvegetation gelebt haben. Bisher waren keine fossilen Funde dieser Tribus bekannt.

Palaeocrassirhinus erinnert im Habitus an zahlreiche heutige Gattungen aus mehreren verwandten Tribus (Anypotactini, Polydrusini, Phyllobiini, Naupactini). Sie alle leben als Imago bevorzugt auf Sträuchern und Bäumen unterschiedlicher Pflanzenfamilien und ernähren sich von Blättern. Es gibt ausgesprochen polyphage (z. B. *Phyllobius pyri* (LINNÉ, 1758)) und oligophage Arten, die z. B. nur an Weiden vorkommen (*Polydrusus corruscus* GERMAR, 1824). Häufig sind sie zur Tarnung grünmetallisch beschuppt, was auch bei einem mir vorliegenden Exemplar aus der Gattung *Paonaupactus* aus dem Baltischen Bernstein erkennbar ist, und flugfähig. Es gibt zahlreiche rezente Vertreter dieser Taxa in den Tropen, wobei es sich oft um Arten handelt, die in Wäldern vorkommen. Ähnliche Bedingungen könnten sie in Messel vorgefunden haben, von wo eine reiche Baum-Flora bekannt ist.

Die Vertreter der Derelomini leben in Palmenblüten, aus denen sie manchmal in großer Anzahl geklopft werden können. Wie ihre Wirtspflanzen finden sich die Vertreter dieser Gruppe weltweit vorwiegend in den Tropen. *Derelomus* erreicht aber heute im Norden an der Zwergpalme *Chamaerops humilis* L. Südfrankreich und Italien. Im Süden geht diese Gattung bis in die Kapprovinz. In der Neotropis ist die Gruppe mit *Celetes* und weiteren Gattungen reich vertreten. Palmen sind aus dem Baltischen Bernstein bekannt. Möglicherweise waren dies Wirtspflanzen von *Protoceletes*.

Viele Molytinae entwickeln sich in Holz oder Früchten und sind besonders in Wäldern anzutreffen, was demnach auch für *Electrotribus* zu vermuten ist.

5. Literatur

Alonso-Zarazaga, M. A. & Lyal, C. H. C. (1999): A world catalogue of families and genera of Curculionoidea (Insecta: Coleoptera) (Excepting Scolytidae and Platypodidae). 315 pp.; Barcelona (Entomopraxis S. C. P. Edition).

Arnoldi, L. V, Zherikhin, V. V., Nikritin, L. M. & Ponomarenko, A. G. (1977): Mezozoyskie Zhestkokrilie. – Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR, **161**: 142–176.

Freude, H., Harde, K. W. & Lohse, A. (1981): Die Käfer Mitteleuropas. Band **10**. 310 pp.; Krefeld (Goecke & Evers).

Heer, O. (1847): Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. Erste Abtheilung: Käfer. – Neue Denkschriften der allgemeinen Schweizerischen Gesellschaft für die gesammten Naturwissenschaften, **8**: 1–229.

Hustache, A. (1942): Un curculionide de l'ambre de la Baltique. – Bulletin Mensuel de la Société Linnéenne de Lyon, **11**: 108–109.

Kuschel, G. (1952): Los Curculionidae de la Cordillera chileno-argentina (1.a parte). – Revista Chilena de Entomologia, **2**: 229–279.

Kuschel, G. (1992): Reappraisal of the Baltic amber Curculionoidea described by E. Voss. – Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, **73**: 191–215.

Kuschel, G. (1995): A phylogenetic classification of Curculionoidea to families and subfamilies. – Memoirs of the Entomological Society of Washington, **14**: 5–33.

Kuska, A. (1992): Three new species of beetles (Coleoptera: Cantharidae, Anobiidae, Curculionidae) from the Baltic amber. – Annals of the Upper Silesian Museum in Bytom – Entomology, **3**: 107–113.

Lutz, H. (1990): Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. – Courier Forschungsinstitut Senckenberg, **124**: 1–165.

Marshall, G. A. K. (1932): Notes on the Hylobiinae (Col. Curc.). – Annals and Magazine of Natural History, (10) **9**: 341–355.

Marshall, G. A. K. (1956): The Otiorrhynchine Curculionidae of the tribe Celeuthetini (Col.). 134 pp.; London (British Museum).

Marvaldi, A. E. & Morrone, J. J. (2000): Phylogenetic systematics of weevils (Coleoptera: Curculionoidea): A reappraisal based on larval and adult morphology. – Entomologica Scandinavica, **31**: 43–58.

Marvaldi, A. E., Sequeira, A. S., O'Brien, C. W. & Farrell, B. D. (2002): Molecular and morphological phylogenetics of weevils (Coleoptera: Curculionoidea): do niche shifts accompany diversification? – Systematic Biology, **51**: 761–785.

Meunier, F. (1921): Die Insektenreste aus dem Lutetien von Messel bei Darmstadt. – Abhandlungen der Hessischen Geologischen Landesanstalt, **7**: 1–16.

POINAR, G. & POINAR, R. (1999): The amber forest: a reconstruction of a vanished world. 239 pp.; Princeton (Princeton University Press).

RHEINHEIMER, J. (2002): Rüsselkäfer – Die artenreichste Tierfamilie der Welt. – Biologie in unserer Zeit, **32** (4): 236–243.

SCHAAL, S. & ZIEGLER, W. (Hrsg.) (1992): Messel – An insight into the history of life and of the earth. 322 pp.; Oxford (Clarendon Press).

SCUDDER, S. H. (1893): Tertiary rhynchophorous Coleoptera of the United States. – Monographs of the United States Geological Survey, **21**: 1–206.

TRÖSTER, G. (1994): Fossile Elateridae (Insecta: Coleoptera) aus dem Unteren Mitteleozän (Lutetium) der Grube Messel bei Darmstadt. – Courier Forschungsinstitut Senckenberg, **170**: 11–64.

VOSS, E. (1953): Einige Rhynchophoren der Bernsteinfauna (Col.). – Mitteilungen aus dem Geologischen Staatsinstitut in Hamburg, **22**: 119–140.

VOSS, E. (1972): Einige Rüsselkäfer der Tertiärzeit aus Baltischem Bernstein (Coleoptera, Curculionoidea). – Steenstrupia, **2** (11): 167–181.

WANAT, M. & BOROWIEC, L. (1986): New genus of weevil (Coleoptera, Curculionidae) from Baltic amber. – Polskie Pismo Entomologiczne, **56** (2): 243–247.

WEITSCHAT, W. & WICHARD, W. (1998): Atlas der Pflanzen und Tiere im Baltischen Bernstein. 256 pp.; München (Verlag F. Pfeil).

WINK, M., MIKES, Z. & RHEINHEIMER, J. (1997): Phylogenetic relationships in weevils (Coleoptera: Curculionoidea) inferred from nucleotide sequences of mitochondrial 16S rDNA. – Naturwissenschaften, **84**: 318–321.

ZHERIKHIN, V. V. (1971): O dolgonosikach (Insecta, Coleoptera) baltiykogo yantarya. – Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR, **130**: 197–209.

ZHERICHIN, V. V. (1992): Tertiary beetles (Insecta, Coleoptera: Curculionoidea), identified from the collections of the Senckenberg Museum. – Senckenbergiana Lethaea, **72**: 169–178.

ZHERICHIN, V. V. & GRATSHEV, V. G. (1995): A comparative study of the hind wing venation of the superfamily Curculionoidea, with phylogenetic implications. In: PAKALUK, J. & SLIPINSKI, S. A. (Hrsg.): Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. CROWSON. Vol. **2**: 633–777; Warsaw (Muzeum i Instytut Zoologii Pan).

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Overview and descriptions of caddisflies (Insecta, Trichoptera) in Dominican amber (Miocene)

Wilfried Wichard

Abstract

In this paper, nine new fossil species of Trichoptera in Dominican amber are described: *Antillopsyche auricula* n. sp., *Antillopsyche digitus* n. sp., *Atopsyche perlucida* n. sp., *Calosopsyche palaeoelegans* n. sp., *Cernotina pulchra* n. sp., *Chimarra (Chimarrita) palaenova* n. sp., *Cubanoptila longiscapa* n. sp., *Macronema hispaniola* n. sp., *Phylloicus velteni* n. sp.

Thus 31 fossil species are verified in Dominican amber. Moreover, there is to be added a specimen of the genus *Ochrotrichia* (Hydroptilidae) which is referred to the extant *Ochrotrichia aldama* (Mosley, 1937), and an innominate female of the Neotropical genus *Austrotinodes*, proving the existence of the family Ecnomidae in Dominican amber. The amber caddisflies are divided into 15 genera and 11 families.

The low occurrence of caddisflies in Dominican amber points at a lack of waters in the tropic mountain forest of Hispaniola at the Miocene, 15–20 million years ago. However, with 12 of 15 genera caddisflies indicate a preference for flowing water. The discussion deals with the reconstruction of aquatic habitats as well as of palaeobiogeographical aspects.

Keywords: Dominican amber, Miocene, Trichoptera, caddisflies, fossil insects, aquatic insects.

Zusammenfassung

In dieser Arbeit werden folgende neun neue fossile Trichoptera-Arten aus dem Dominikanischen Bernstein beschrieben: *Antillopsyche auricula* n. sp., *Antillopsyche digitus* n. sp., *Atopsyche perlucida* n. sp., *Calosopsyche palaeoelegans* n. sp., *Cernotina pulchra* n. sp., *Chimarra (Chimarrita) palaenova* n. sp., *Cubanoptila longiscapa* n. sp., *Macronema hispaniola* n. sp., *Phylloicus velteni* n. sp.

Damit sind insgesamt 31 fossile Arten im Dominikanischen Bernstein nachgewiesen. Hinzu kommt eine weitere Köcherfliege, die nach morphologischen Kriterien der rezenten *Ochrotrichia aldama* (Mosely, 1937) angehört. Darüber hinaus liegt ein nicht näher beschriebenes Weibchen der neotropischen Gattung *Austrotinodes* vor, die die Anwesenheit der Familie Ecnomidae im Dominikanischen Bernstein bekundet. Die Köcherfliegen verteilen sich auf 15 Gattungen in 11 Familien.

Das geringe Vorkommen von Köcherfliegen im Dominikanischen Bernstein weist auf einen Mangel an Gewässern hin, der offensichtlich im Miozän vor 15–20 Millionen Jahren im tropischen Bergwald von Hispaniola vorherrschte. Andererseits zeigen 12 von insgesamt 15 Gattungen eine deutliche Präferenz für fließende Gewässer. Diskutiert wird die Rekonstruktion der aquatischen Habitate ebenso wie paläobiogeographische Aspekte.

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1. Introduction

In Dominican amber inclusions of caddisflies are rarely found. Extrapolations revealed that only about 0.1% of enclosed insects that are found in Dominican amber belong to the order Trichoptera (WICHARD 1987). The BRODZINSKY-PENHA collection of Dominican amber at the National Museum of Natural History, Smithsonian Institution, in Washington, D.C. consists of more than 5,000 amber pieces. Most pieces are syninclusion-stones, representing some 20,000 inclusions (POINAR & POINAR 1994) and a wide range of fossil animals and plants. But caddisflies are lacking in this famous Dominican amber collection (HENWOOD 1993). POINAR & POINAR (1999) have a further Dominican amber collection of about 3,000 random pieces with inclusions and found eight Trichoptera. With an amount of 0.4% of all enclosed insects, caddisflies are represented exceptionally frequently.

Nevertheless, in the course of the last 25 years far more than a hundred amber pieces with caddisflies provide evidence. Many of them could be assigned to families or genera, and altogether 22 species are described until now (WICHARD 1981, 1983a, b, 1985, 1986, 1989, 1995a, b, 2000, JOHANSON & WICHARD 1996, WELLS & WICHARD 1989). This paper diagnoses new species and completes older descriptions. It gives an overview of all known caddisflies in Dominican amber, and tries to draw preliminary conclusions about the aquatic biota of Hispaniola 15–20 million years ago at Miocene period in which the Dominican amber originated (ITURRALDE-VINENT & MACPHEE 1996, ITURRALDE-VINENT 2001).

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2. Material and methods

The fossil caddisflies of Dominican amber, which are redescribed in this paper, are originally deposited in the collection of "Staatliches Museum für Naturkunde Stuttgart" and in the private amber collection of W. Wichard, Bonn. Additional caddisflies of Dominican amber were included that reside in the amber collection of the American Museum of Natural History, New York and of the Oregon State University Corvallis. All new holotypes belong exclusively to the collection of the Staatliches Museum für Naturkunde Stuttgart.

In order to prepare some pieces for identification and description, the amber was cut, face-grinded, and polished using a cutting machine and a polishing machine "RotoPol-25 Struers" with grinding paper for metallography: Grip 800, 1200, 2500, and 4000. Suitable amber pieces were embedded in synthetic resin ("Casring Resin GTS Vosschemie" together with "MEKP-Hardener Vosschemie") to guarantee for a protection of the holotypes and paratypes.

The state of both, the Dominican amber pieces and the embedded inclusions is not always of equal quality. Most of the fossil caddisflies are incompletely preserved. Legs and antennae are frequently either missing or damaged. In many cases the saddleback roof-like wings cover the abdomen and the outer genitalia in such a way as to render a complete description and documentation impossible. Important venations of the hindwings are oftentimes not available since the hindwings are covered dorsally by the forewings and from the bottom by the abdomen. In addition, the foldings of the wings render the reconstruction difficult or even impossible.

Detailed drawings and colour pictures were made for the documentation of the amber-caddisflies. The macroscope Leica M420 with apozoom 1:6 was used in combination with a SLR-camera Minolta X300 and slide-film Kodak Ektachrome 64T for exposure with tungsten illumination (3200° K). Single lighting was provided by two Schott (KL 1500 electronic) cold light-lamps with two-armed, flexible light conductors per side.

In the concluding discussion attempts are made to reconstruct habitats of the fossil amber caddisflies on the basis of the "principle of actuality": The Present is the Key to the Past. Very probably fossil and extant genera display similar behaviour in adaptation to their habitats, and thus they potentiate the reconstruction of habitats.

Abbreviations

I–V	fork I–V in forewing and hindwing
dc	discoidal cell
mc	median cell
tc	thyridium cell

Acronyms of depositories

AMNH	American Museum of Natural History, New York
BMNH	Natural History Museum, London
GPIMH	Geological-Palaeontological Museum, University of Hamburg
NMNH	National Museum of Natural History, Washington D. C.
OSUC	Oregon State University, Corvallis
SMNS	Staatliches Museum für Naturkunde Stuttgart

3. Systematics and classification

Order Trichoptera Kibry, 1813
Suborder Spicipalpia Weaver, 1983
Family Hydrobiosidae Ulmer, 1905
Genus *Atopsyche* Banks, 1905

Type species: *Atopsyche tripunctata* Banks, 1905

Diagnosis (Ross & King 1952, Schmid 1989). – Ocelli present; maxillary palps 5-segmented, with terminal segment elongate, and without cross striations. Forewing without median cell, M forked at about half way to wing margin, fork III (M_{1+2}) and IV (M_{3+4}) petiolate. Middle tibia with preapical spurs, tibial spurs: 2, 4, 4.

Male: Long processes on 6th and 7th sternum. Inferior appendages 2-segmented, basal segment always longer than apical segment.

Remarks. – The southern hemisphere disjunction of *Atopsyche* is very pronounced, from southwestern states of the United States, through Central America, including the Antilles, and mainly South America, except the Chile region where another hydrobiosid genus is represented. Flint et al. (1999) and Holzenthal & Cressa (2002) listed 117 + 3 = 120 species. Their larvae are free-living predators in streams and rivers of the Neotropical region. *Atopsyche* is complementary distributed compared with the genus *Rhyacophila,* which larvae live as predators in running waters of the northern hemisphere. Rhyacophilidae and Hydrobiosidae are sister groups.

Atopsyche perlucida n. sp.

Figs. 1a–b, 2

Holotype: Male embedded in Dominican amber; SMNS: Do-5711 (ex Coll. Wichard). The left side of the holotype is well preserved in clear amber which is embedded in synthetic resin. The forewings cover the hindwings, the genitalia can be seen in lateral view through the wings, as far as possible.

Etymology: Perlucidus = transparent: The transparent wings make it possible to describe the male genitalia, as far as possible.

Diagnosis. – In forewing and male genitalia the new species is similar to the extant *A. rinconi* Holzenthal & Cressa, 2002 found in Venezuela, but differs in the shape of the inferior appendages. The first segment of inferior appendages *Atopsyche perlucida* n. sp. is slender and very long, basal narrow, easily twisted; the second segment is also slender and 1/3 of first segment in length.

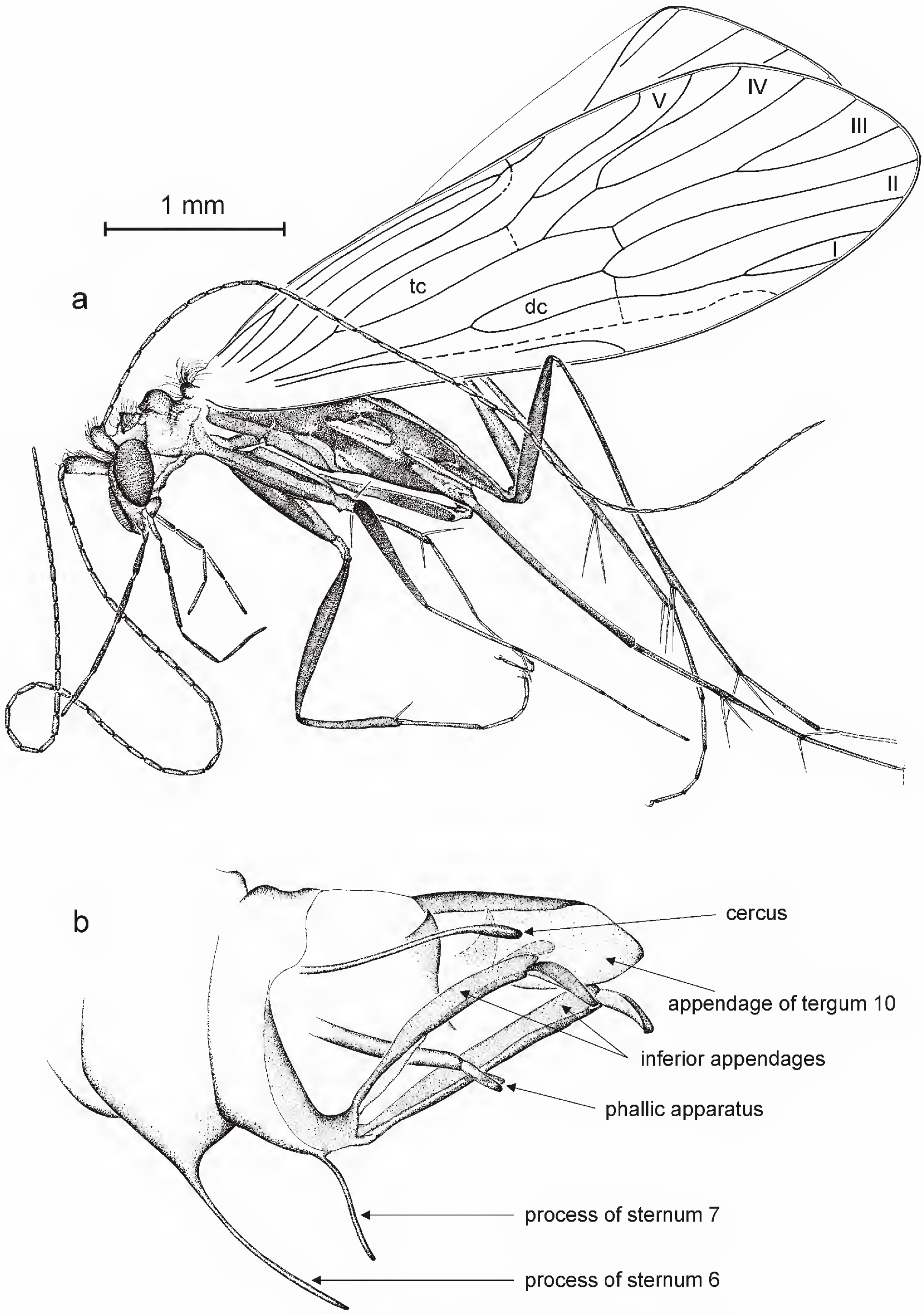

1 mm
a
V
IV
III
II
I
tc
dc
b
cercus
appendage of tergum 10
inferior appendages
phallic apparatus
process of sternum 7
process of sternum 6

Fig. 1. *Atopsyche perlucida* n. sp., male, holotype; SMNS: Do-5711 (ex Coll. WICHARD); **a**: lateral view; **b**: genitalia in lateral view.

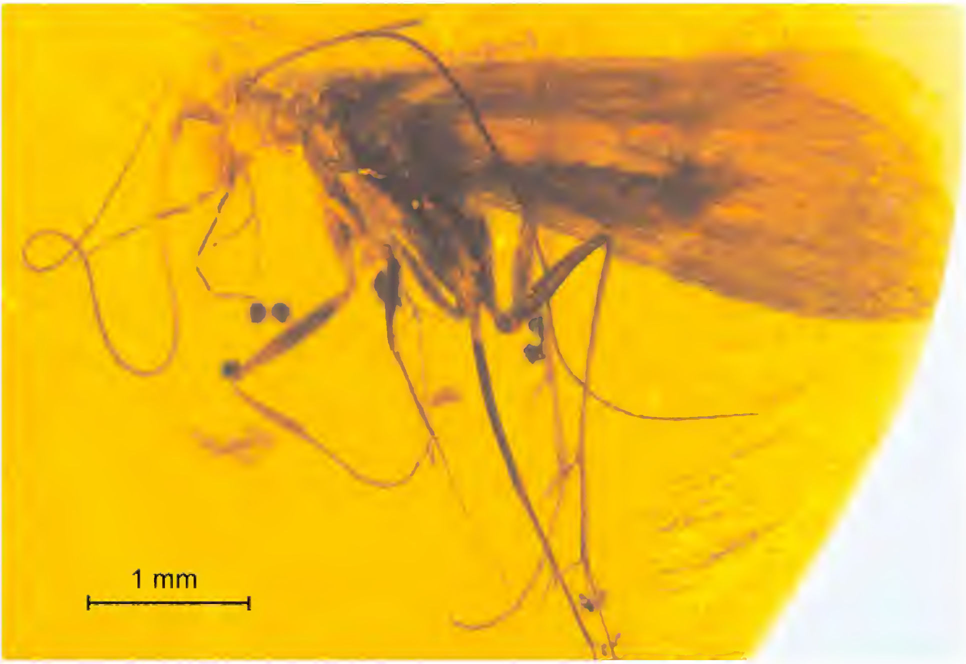


Fig. 2. *Atopsyche perlucida* n. sp., male in lateral view, holotype; SMNS: Do-5711 (ex Coll. WICHARD).

Description. – Length of forewing: 4.2 mm. Adults with ocelli. Maxillary palps 5-segmented, long; second segment slender cylindrical formed as the first segment; segment three, four and five longer than segment one and two. Tibial spurs: 2, 4, 4. In forewing radius R_1 seems to be unbranched. Fork I ($R_2 + R_3$) and fork II ($R_4 + R_5$) are present (Fig. 1a). Fork I is petiolate, the stem is as long as fork I and as well as the discoidal cell. Discoidal cell is closed. Fork II is sessil and originates at the distal crossvein (r_{2+3}-r_4) of the discoidal cell. Fork III ($M_1 + M_2$) and IV ($M_3 + M_4$) present, both petiolate. Thyridium cell seems to be closed, the bifurcation of media M in M_{1+2} and M_{3+4} with a short stem. Also fork V (Cu1a + Cu1b) with a short stem. Cubitus Cu2 long, fused anal veins (1A + 2A + 3A), with crossvein near apex forming a small cell on posterior margin of wing. Hindwings are covered and not suitable for description.

Male genitalia behind the hyaline wings is tried to be described from lateral view (Fig. 1b): 6th and 7th sternum each with prominent spine-like ventral process on posteromesal margin; process on 7th sternum short, slender, sigmoidal, process on 6th sternum longer, slender, easily curved. 9th segment narrow, parapod seems to be sclerotized with a prominent spine apicodorsad, margins sigmoidal. The long and slender cercus ends with a small ampule-like amplification. Preanal appendages seem to be covered. Proctiger, in lateral view, broadly widened apically. Inferior appendages (claspers) with first segment slender and very long, basal narrow, easily twisted, mesal and apical of uniform width. The second segment slender, 1/3 of first segment in length. Phallic apparatus is impossible to describe behind the hyaline wings.

Remarks. – *Atopsyche perlucida* n. sp. is the first fossil species of the genus and embedded in Miocene Dominican amber.

Family Glossosomatidae WALLENGREN, 1891

Genus *Cubanoptila* SYKORA, 1973

Type species: *Cubanoptila cubana* SYKORA, 1973

Diagnosis (SYKORA in BOTOSANEANU & SYKORA 1973). – Typical traits which characterize the fossil forms of the genus *Cubanoptila* are antennae, maxillary palps, tibial spurs, and the male genitalia. Ocelli present. Antennae filiform with differentiations of the first three segments: First segment (scapus) robust and long, second segment (pedicellus) small and nodular, third segment about as long as segment four plus five, inside concave with a row of few spines. Maxillary palps 5-segmented, third segment large, bulged out, kidney-shaped, inside with densely packed short hairs constructed to a brush. Tibial spurs: 0, 4, 4. In forewing R_2 and R_3 form fork I, R_4 and R_5 form fork II; discoidal cell closed; fork I is sessil, fork II petiolate; media M_1 and media M_2 form a petiolate fork III, media M_{3+4} simple, not forked, fork IV absent.

Male genitalia: Both inferior appendages (claspers) forming a ventral capsule, well sclerotized or membranous and transparent. Inside run two pairs of dark spines, long and curved, probably of 10th segment; the upper pair much more developed than the lower pair, caudally protruded, forming a small tongue-like membrane. Lateral superior appendages of 9th segment consisting of spines and lobes, with a typical dark spine oriented dorsad. Dorsal part of 10th segment forms a pair of distal appendages, each laterally with a fine long stylus bearing a long seta.

Remarks. – With five extant species, the genus *Cubanoptila* occurs exclusively on the island of Cuba. It is remarkable that the endemic genus is also represented by four species in the Miocene Dominican amber on the neighbouring island Hispaniola, whereas extant species of *Cubanoptila* are missing on Hispaniola, so far.

Key to the four fossil *Cubanoptila* species

1 Scapus as long as the eye-diameter 2
– Scapus much longer than the eye-diameter 3
2 Dorsodistal appendages of 10th segment forming a small edge .... ***poinari***
– Dorsodistal appendages of 10th segment narrow to a rounded tip .... ***mederi***
3 Third antennal segment caviform inside with a row of few spines .... ***grimaldii***
– Third antennal segment not caviform inside and without spines .... ***longiscapa* n. sp.**

Cubanoptila longiscapa n. sp.

Figs. 3, 4

Holotype: Male arranged in a clear Dominican amber piece which is embedded in synthetic resin and can be seen in ventral and dorsal view. The forewings cover the hindwings and laterodorsally the male genitalia, which can be seen in ventral view. SMNS: Do-5712 (ex Coll. WICHARD).

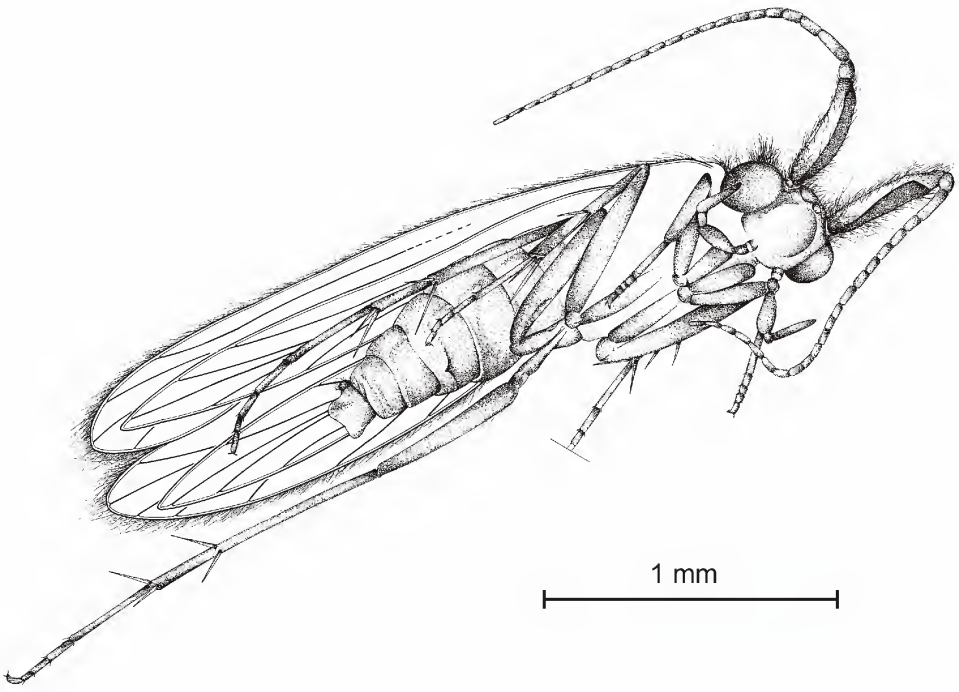


Fig. 3. *Cubanoptila longiscapa* n. sp., male in ventral view, holotype; SMNS: Do-5712 (ex Coll. WICHARD).

Etymology: Longus = long: The Scapus, the first antennal segment, is unusual long compared with the scapi of all other fossil species of *Cubanoptila*.

Diagnosis. – The new species differs from all other described fossil species by a reduction of the 3rd segment of the maxillary palps. This segment is barely bulged, not bearing a brush and is smaller than the 5th segment.

Description. – Length of forewing: 2.3 mm. General structure and forewing venation typical of genus. Ocelli present. Antennae filiform with typical differentiations of the first three segments: Scapus twice as long as the eye-diameter, ventrally a dark and slender brush runs parallelly; pedicellus small and nodular; 3rd segment long, but not formed caviform and without any spines. The 3rd segment of the maxillary palps is smaller than 5th segment, barely bulged, not bearing a brush, shortened, atypical and without function probably usual in genus *Cubanoptila*. Male genitalia are covered ventrally by a capsule composed of both inferior appendages (claspers).

Discussion. – The four fossil species of genus *Cubanoptila* from Dominican amber differ in the male genitalia, in the structures of the antennae, and the maxillary palps:

C. mederi WICHARD, 1989 (Figs. 5a–c, 6) and *C. poinari* WICHARD, 1989 (Figs. 7a–d, 8) possess antennae with the typical differentiation of the first three segments: the scapus is approximately as long as the eye-diameter, the pedicellus is small and nodular, the third segment is as long as segments four plus five, inside concave with

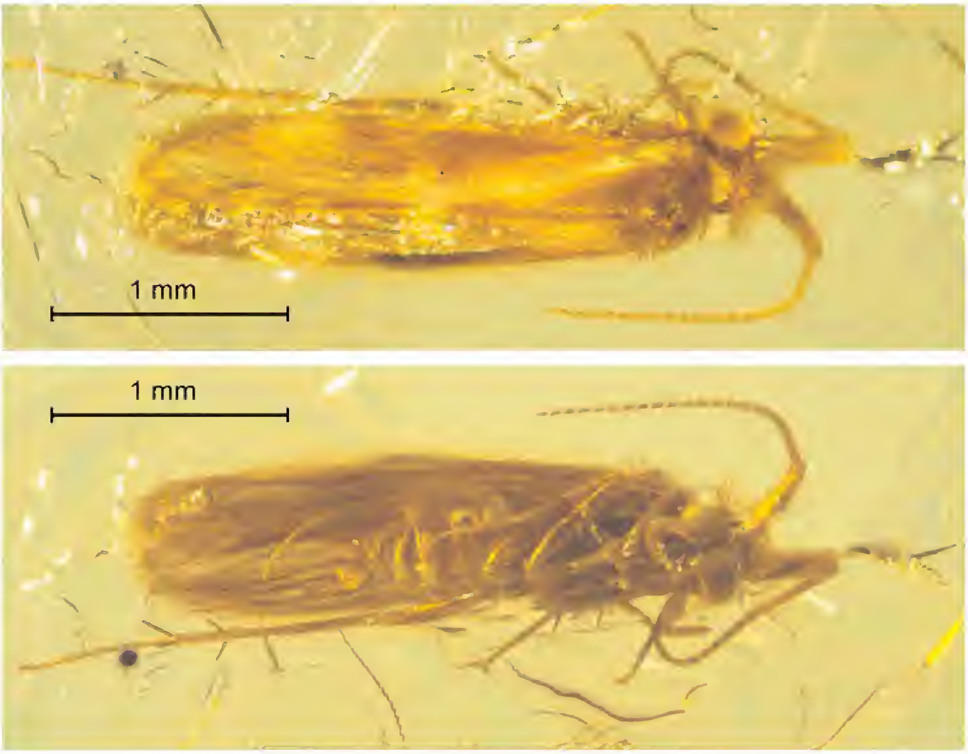


Fig. 4. *Cubanoptila longiscapa* n. sp., male in dorsal and ventral view, holotype; SMNS: Do-5712 (ex Coll. WICHARD).

a row of few spines. The third segment of the maxillary palps is the largest of the five segments, kidney-shaped and inside densely packed with small dark hairs bundled to a brush. *C. mederi* and *C. poinari* differ in the male genitalia, leastwise at two genital structures. 1. The lateral dark spine oriented dorsad (appendage of 9th segment?) is in *C. poinari* formed short and straight, whereas in *C. mederi* the spine is longer and slightly sigmoidal. 2. Both dorsodistal appendages of 10th segment form a small edge in *C. poinari*, whereas in *C. mederi* the appendages taper into a rounded tip.

C. grimaldii WICHARD, 1995 and *C. longiscapa* n. sp. (Figs. 3, 4) differ from *C. mederi* and *C. poinari* by the first antennal segment (scapus) which is longer than the eye-diameter, in *C. longiscapa* n. sp. about twice as long as the eye-diameter. In *C. grimaldii* the long antennal third segment is formed caviform inside with a row of few spines (WICHARD 1995a). In *C. longiscapa* n. sp. this segment is not formed caviform inside and is without spines.

Possibly, the third segment of the antennae and the third segment of the maxillary palps form a functional complex. The brush of the maxillary palps could possibly clean the concave insides of the antennal third segments and their rows of spines, which possibly are sensillae. Both structures are well developed in fossil forms (e.g. *C. mederi*, *C. poinari*), but they were step by step reduced *(C. grimaldii)*, probably with the loss of a functional brush of the maxillary palps in *C. longiscapa* n. sp. and in recent forms.

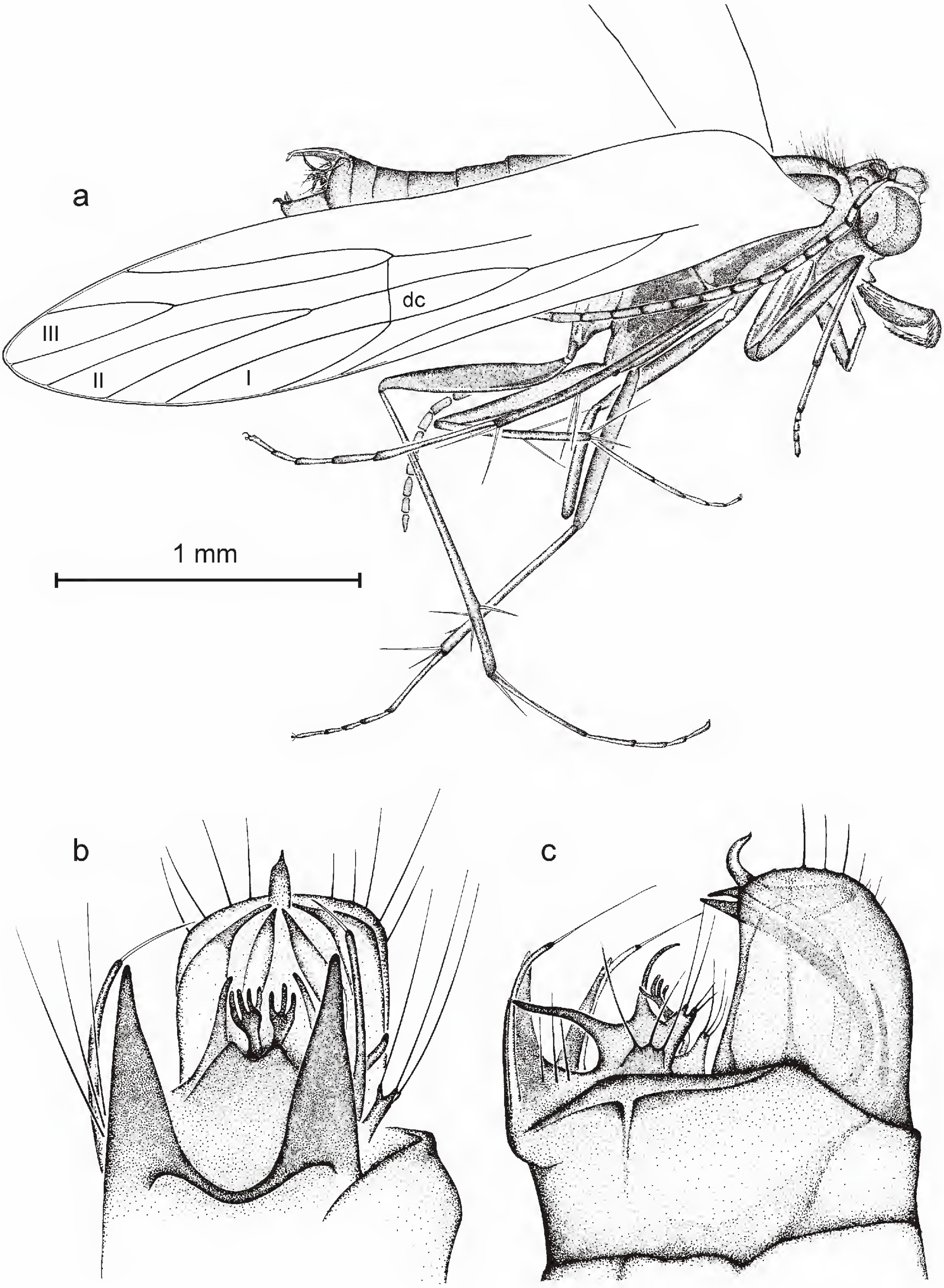


Fig. 5. *Cubanoptila mederi* Wichard, 1989, male; SMNS: Do-4144-M; **a**: lateral view; **b**: genitalia in dorsal view; **c**: genitalia in lateral view.

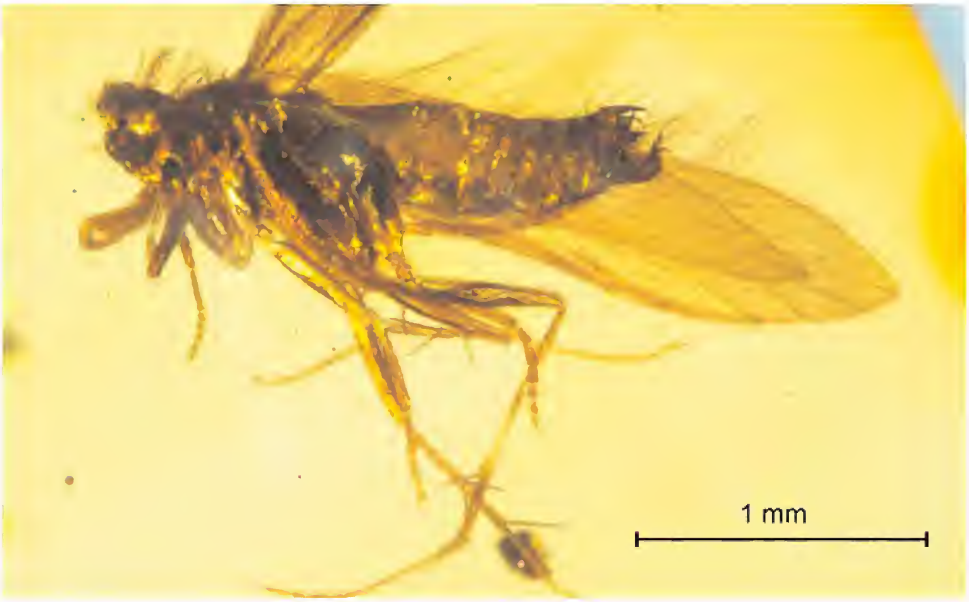


Fig. 6. *Cubanoptila mederi* WICHARD, 1989, male in lateral view; SMNS: Do-4144-M.

Suborder Annulipalpia MARTYNOV, 1924
Family Philopotamidae STEPHENS, 1829
Genus *Chimarra* STEPHENS, 1829

Type species: *Phryganea marginata* LINNAEUS, 1767

Diagnosis (BLAHNIK 1998). – Head with frontal setal wart, with anteromesal, anterior, posterior, and posterolateral setal warts, 3 ocelli present, antennae with simple scapi and unmodified flagellar segments. Labial palps 3-segmented. Maxillary palps 5-segmented, first segment very short, second and third segments relatively long, fourth segment relatively short, and fifth segment varying in length; second segment with several bristlelike setae apicomesally. Foreleg with one tibial spur, tibial spurs: 1, 4, 4. Forewing venation with absence of media M_4, fork I, II, III, V are present. Discoidal cell, thyridium cell and median cell closed. Hindwing with fork I and II (fork I absent in subgenus *Otarrha*), fork III mostly present, but absent in subgenus *Otarrha* and in some species of subgenus *Chimarra* and subgenus *Chimarrita*, fork V ever present. Anal veins in hindwing forming a closed cell, anal vein 2A looped to anal vein 1A.

Male genitalia: Inferior appendages (claspers) one-segmented. 10th tergum partially or completely divided into two lobes mesally or (subgenus *Curgia*) entire knoblike, cleft (lobes divided not mesally). Preanal appendages (cerci) absent or fused basally, knoblike, stylus short or large, flattened, and earlike. Ventral process of 9th sternum acute, triangular, or/and elongated.

Remarks. – The genus is worldwide spread with a number of species that would probably exceed far more than 400. The Neotropical species are distributed into four

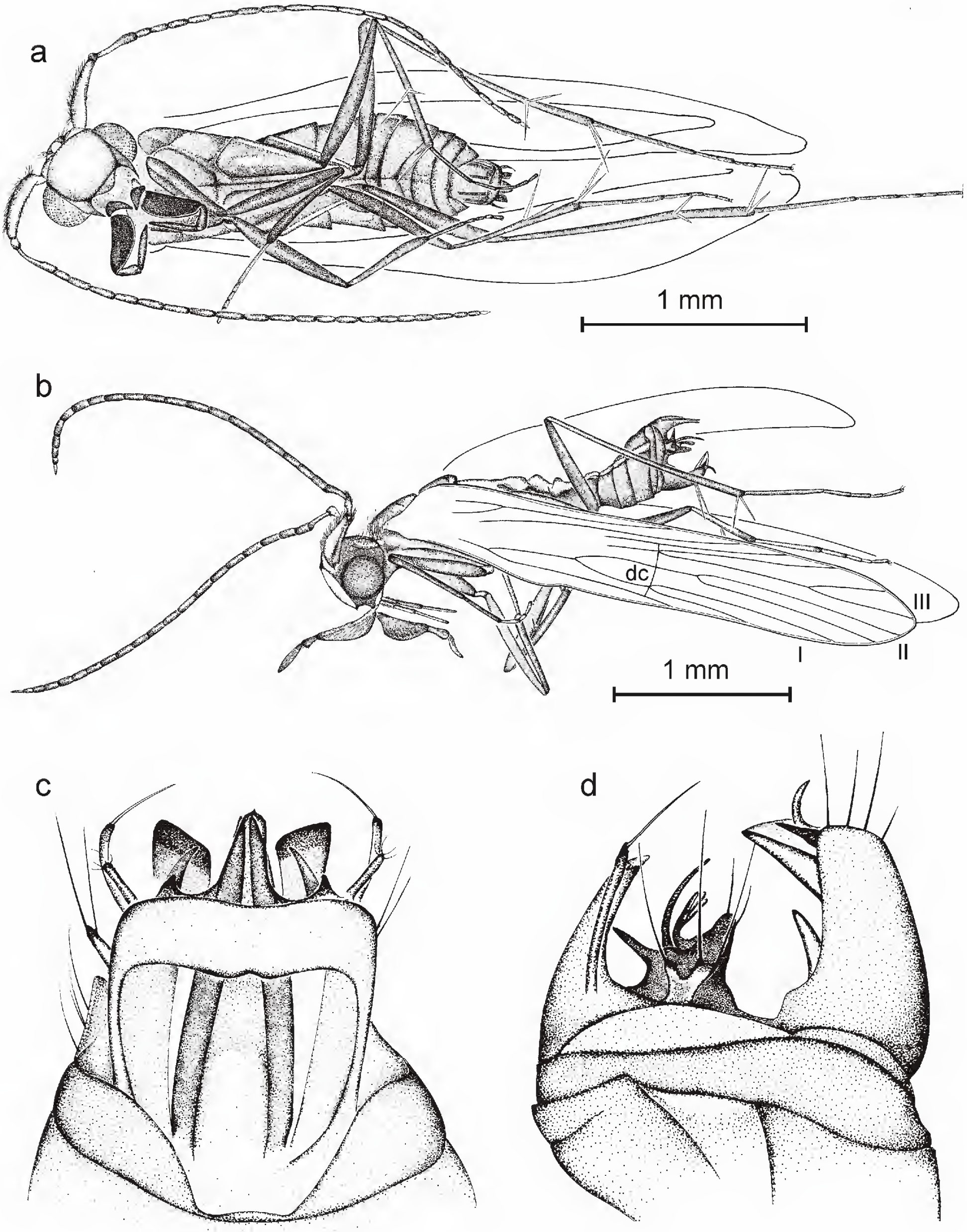


Fig. 7. *Cubanoptila poinari* Wichard, 1989, males; **a**: ventral view; SMNS: Do-5344-M; **b–d**: Coll. Wichard, Bonn; **b**: lateral view; **c**: genitalia in ventral view; **d**: genitalia in lateral view.

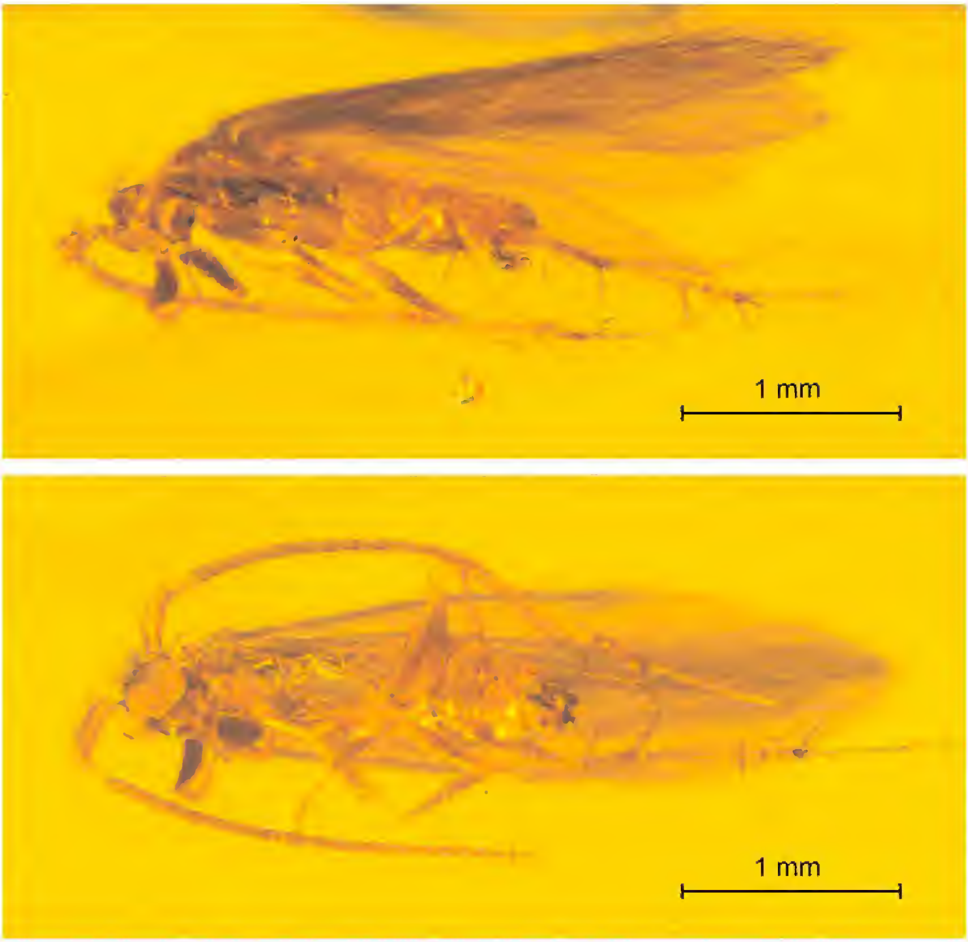


Fig. 8. *Cubanoptila poinari* WICHARD, 1989, male in lateral and ventral view; SMNS: Do-5344-M.

subgenera: *Chimarra* STEPHENS, 1892, revised by BLAHNIK 1998, *Curgia* WALKER, 1860, revised by FLINT 1998, *Chimarrita* BLAHNIK, 1997 and *Otarrha* BLAHNIK, 2002.

Subgenus *Chimarrita* BLAHNIK, 1997

Type species: *Chimarra simpliciforma* FLINT, 1971

Diagnosis (BLAHNIK 1997). – General genus structures and some following additional structures:

- Forewing stem of radial sector Rs vein is straight, without curvature.
- Forewing crossveins s, rm and m nearly linearly arranged.
- Forewing anal vein 2A forked, 3A looped to 2A or 3A, all together merging.

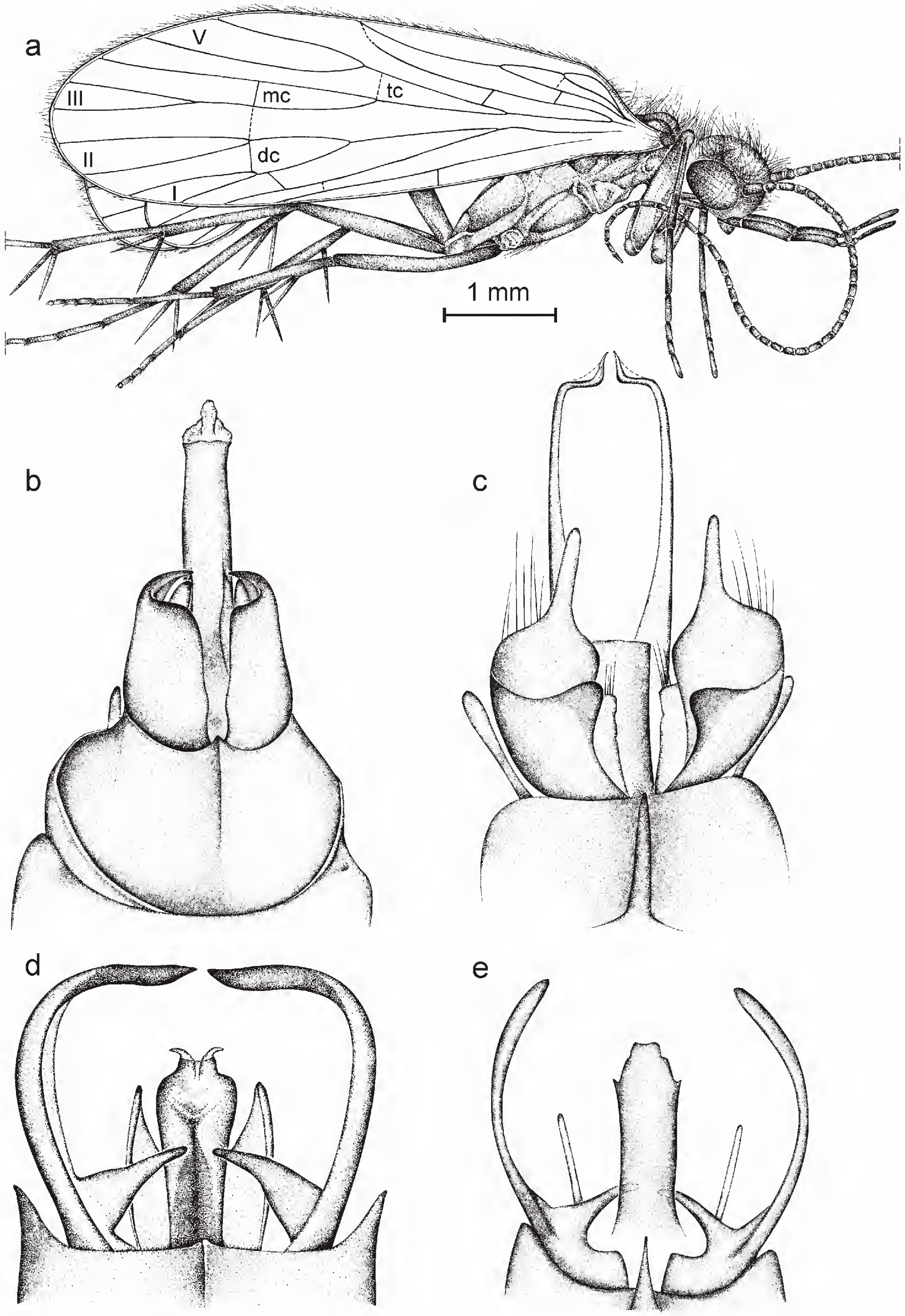


Fig. 9. a: *Chimarra (Chimarrita) weitschati* Wichard, 1983, male in lateral view, holotype; GPIMH: 2534; **b**: *Chimarra (Chimarrita) palaedominicana* Wichard, 1983, male genitalia in ventral view, holotype; SMNS: Do-5706 (ex Coll. Wichard); **c**: *Chimarra (Chimarrita) dommeli* Wichard, 1983, male genitalia in ventral view, holotype; SMNS: Do-5707(ex Coll. Wichard); **d**: *Chimarra (Chimarrita) weitschati* Wichard, 1983, male genitalia in ventral view, holotype; GPIMH: 2534; **e**: *Chimarra (Chimarrita) resinae* Wichard, 1983, male genitalia in ventral view, holotype; SMNS: Do-5705 (ex Coll. Wichard).

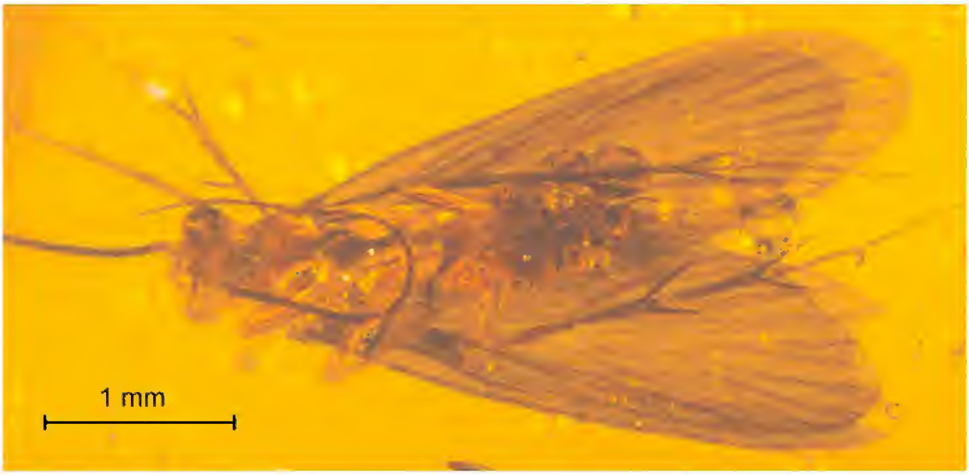


Fig. 10. *Chimarra (Chimarrita) resinae* WICHARD, 1983, male in ventral view, holotype; SMNS: Do-5705 (ex Coll. WICHARD).

– Hindwing radial sector Rs is 4-branched, media M 2- or most 3-branched.

– Hindwing radius R_1 is not fused with subcosta Sc.

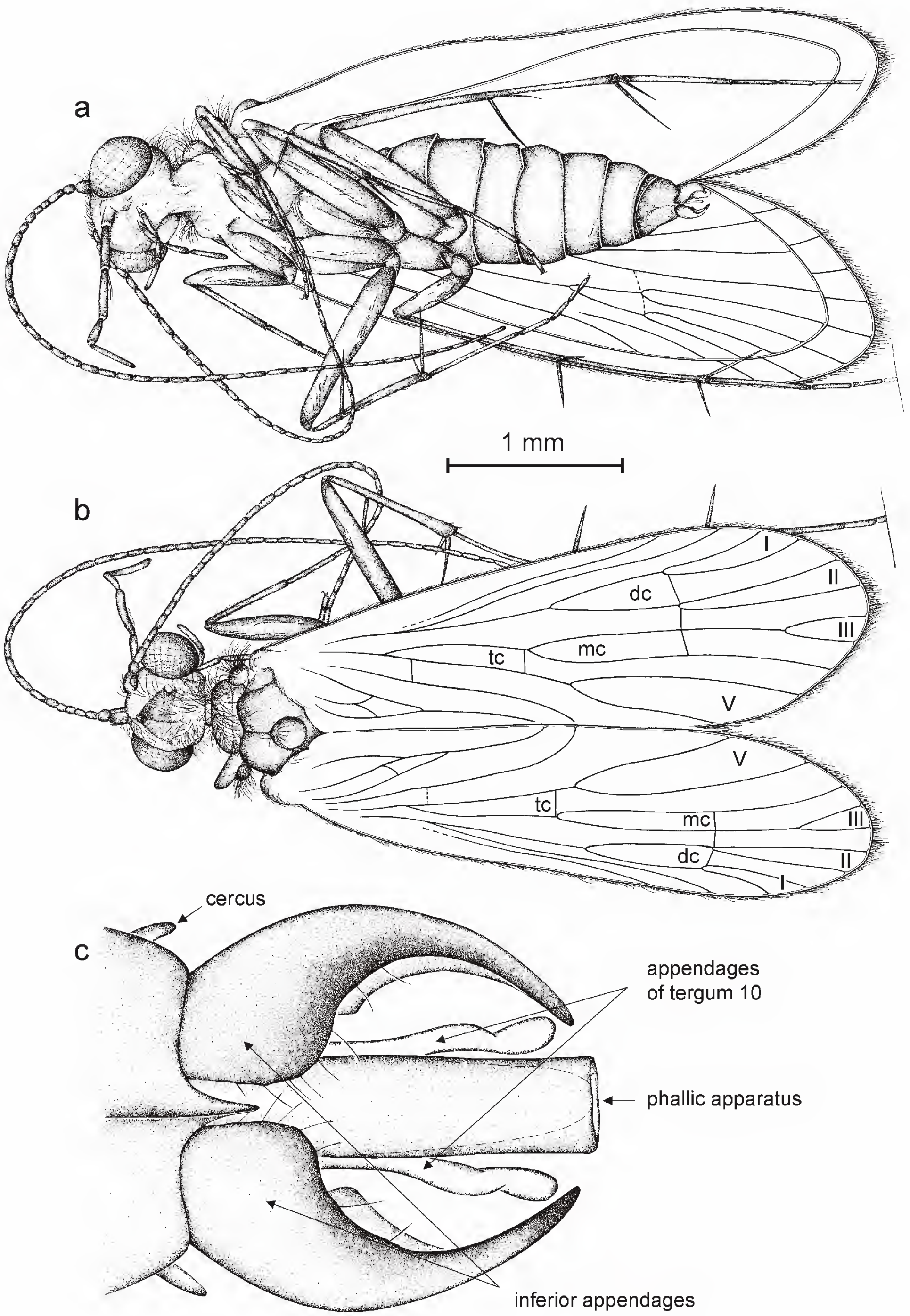
– Male genitalia 10th tergum is partially or completely divided and widely separate.

– Male genitalia ventral process of 9th sternum is acute and elongate.

Remarks. – In Dominican amber six species of *Chimarra* have been found belonging to the subgenus *Chimarrita*:
Chimarra (Chimarrita) dommeli WICHARD, 1983 (Fig. 9c)
Chimarra (Chimarrita) palaedominicana WICHARD, 1983 (Fig. 9b)
Chimarra (Chimarrita) succini WICHARD, 1983 (Figs. 11a–c)
Chimarra (Chimarrita) resinae WICHARD, 1983 (Figs. 9e, 10)
Chimarra (Chimarrita) weitschati WICHARD, 1983 (Figs. 9a, 9d)
Chimarra (Chimarrita) palaenova n. sp. (Figs. 12a–d, 13)

Key to fossil *Chimarra (Chimarrita)* species

1 Hindwing media M 2-branched, without fork III and IV .... *succini*
– Hindwing media M 3-branched, with fork III, without fork IV 2
2 One-segmented clasper forming two branches 3
– One-segmented clasper forming domed cover 4
3 Tips of both curved branches nearly touch mediad .... *weitschati*
– Tips of both curved branched do not touch mediad .... *resinae*
4 Apical margin of clasper with a finger-like appendage .... *dommeli*
– Apical margin of clasper without finger-like appendage 5
5 Phallic apparatus overtopping the apical level of the genitalia .... *palaedominicana*
– Phallic apparatus not overtopping the apical level of the genitalia .... *palaenova* **n. sp.**


a
1 mm
b
I
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dc
III
tc
mc
V
V
tc
III
mc
dc
II
I
cercus
c
appendages
of tergum 10
phallic apparatus
inferior appendages

Fig. 11. *Chimarra (Chimarrita) succini* Wichard, 1983, male, holotype; SMNS: Do-3386-M-1 (ex Coll. Wichard); **a**: ventral view; **b**: dorsal view; **c**: genitalia in ventral view.

Chimarra (Chimarrita) succini Wichard, 1983

Figs. 11a–c

Holotype: Male embedded in Dominican amber; SMNS: Do-3386-M-1.

Diagnosis. – Unusually, *Chimarra succini* has a 2-branched media M in hindwing instead of 3-branched media M. Hindwings with media M 2-branched is an apomorphy of subgenus *Otarrha* and also found in some species of subgenus *Chimarra* and subgenus *Chimarrita.* Nevertheless *Chimarra succini* does not belong to subgenus *Chimarra* or subgenus *Otarrha* because:

- *C. succini* posseses fork I in hindwing,
- radius R_1 is not fused with subcosta in hindwing,
- stem of radial sector Rs is straight, without curvature,
- crossveins s, rm and m are nearly linearly arranged.

The four characteristics assigned *C. succini* to the subgenus *Chimarrita.*

Description. – Original description by Wichard (1983b), fossil *Chimarra (Chimarrita) succini* is refigured and described for completeness and for comparison with the species belonging to the subgenus *Chimarrita.*

Forewing length: 3.5 mm. In forewing (Fig. 5a) stem of radial sector Rs not curved, but straight and nearly parallel to subcosta Sc. Crossveins s, rm and m nearly linearly arranged. Fork I, II, III, V are present. Anal vein 2A apparently forked to 1A, 2A, and 3A with crossvein, 3A merging with 1A-2A relatively distally. In hindwing radius R_1 not fused to subcosta Sc. Radial sector Rs 4-branched, media M 2-branched, without fork III und IV. Fork I, II, V are present.

Male genitalia (Figs. 5b–c): Ventral process of 9th sternum acute and triangular. The inferior appendage (clasper) is one-segmented, at the basis wide and domed, the distal part mesad curved and tapered, inside deepened. The preanal appendage (cercus) is formed as a short, rounded pin. 10th tergum probably nearly completely divided into two elongated finger-like styli, mesoventrad. At their basis both styli probably fused.

Chimarra (Chimarrita) palaenova n. sp.

Figs. 12a–d, 13

Holotype: Male embedded in Dominican amber (Fig. 12c–d); SMNS: Do-5713 (ex Coll. Wichard).

Paratypes: Four males embedded in Dominican amber; one is kept in collection G. Poinar, OSUC (Figs. 12a–b, 13); one in the amber collection W. Wichard, Bonn; two in the SMNS: Do-4121-M, Do-5718.

Etymology: Old and new, a sudden new fossil species of genus *Chimarra (Chimarrita).*

Diagnosis. – *Chimarra (Chimarrita) palaenova* n. sp. seems to be closely related to the fossil *C. (C.) palaedominicana* in male genitalia. They have constructive similarities in the inferior appendages (claspers) but differ in the size of the phallic apparatus, which protrude twice the length from the level of the genitalia in *C. (C.) palaedominicana*, whereas in *C. (C.) palaenova* n. sp. the phallic apparatus reaches the apical level of the genitalia.

Description. – Forewing length: 4.8 mm. Typical general structures of genus *Chimarra.* Fig. 12b shows the front of the head with the dominant eye-pair, the first

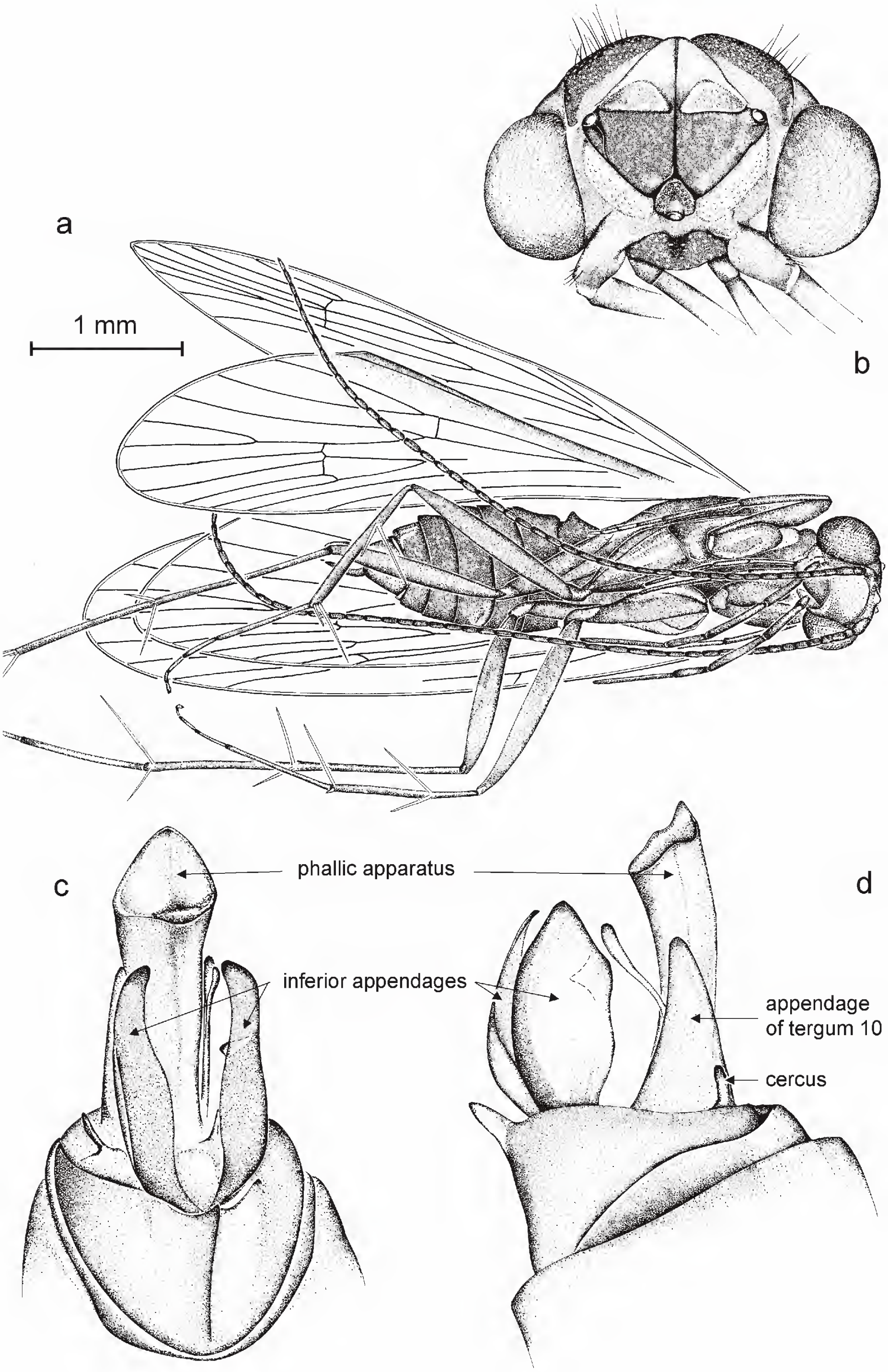
a
1 mm
b
c
phallic apparatus
d
inferior appendages
appendage of tergum 10
cercus

Fig. 12. **a–b**: *Chimarra (Chimarrita) palaenova* n. sp., male, paratype; Coll. Poinar, OSUC; **a**: ventral view; **b**: forehead; **c–d**: *Chimarra (Chimarrita) palaenova* n. sp., male, holotype; SMNS: Do-5713 (ex Coll. Wichard); **c**: genitalia in ventral view; **d**: genitalia in lateral view.

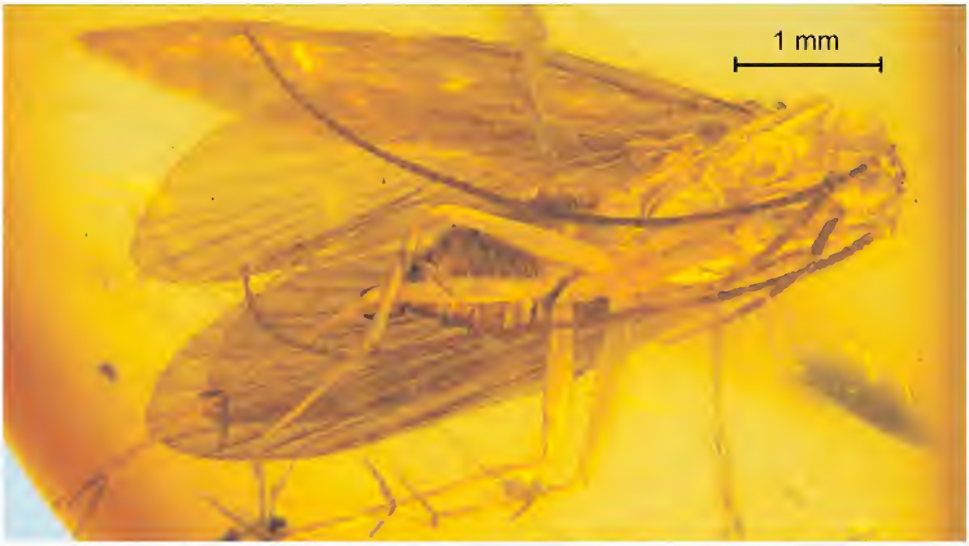

Fig. 13. *Chimarra (Chimarrita) palaenova* n. sp., male in ventral view, paratype; Coll. Poinar, OSUC.

antennal segments (scapi), the three ocelli and the typical setal warts of the head capsule. The frontal setal wart is arranged between the antennal scapi. The median ocellus is surrounded by the anteromesal setal wart. Between the compound eyes the three ocelli mark and border a right-angled triangle, which is sclerotized and slightly brown coloured. This triangular sclerotized field is surrounded by setal wards. Both legs (sides) of the triangle are flanked right and left by the anterior setal warts, and the two posterior setal warts run back-to-back along the hypotenuse. The large posterolateral setal warts dorsally round off the warts-rich forehead. The labial palps are 3-segmented. The maxillary palps are 5-segmented; first short, second and third segment identically long, fourth segment shorter, and fifth segment a little longer than second or third segment. Second segment with some bristlelike setae apicomesally.

In forewing (Fig. 12a) vein R_1 runs parallelly to subcosta Sc, the stem of Rs vein is straight, without curvature, crossveins s, r-m and m are nearly linearly arranged and pigmentation is lacking. Fork I, II, III, and V are present. Discoidal, median, and thyridium cells are closed, m-cu also without pigmentation. Anal vein 2A forked, 3A looped to 2A, all together merging relatively distally. In hindwing radius R_1 runs parallelly to subcosta. Fork I, II, III, and V are present. Tibial spurs formula: 1, 4, 4.

In male genitalia (Figs. 12c–d) ventral process of 9th sternum is small, acute, and triangular. Cercus (preanal appendage) is short and finger-like. 10th tergum is completely divided into two elongated and triangular styli which flank the phallic apparatus at both sides. Distally each triangular stylus possesses an elongated lobe, which is curved mesoventrad. The inferior appendages (claspers) are elongated, slightly twisted, slightly curved mesodorsad, and ending in a dark tip.

Family Hydropsychidae CURTIS, 1835
Subfamily Hydropsychinae CURTIS, 1835
Genus *Calosopsyche* ROSS & UNZICKER, 1977

Type species: *Hydropsyche calosa* BANKS, 1938

Diagnosis (ROSS & UNZICKER 1977, FLINT & BUENO SORIA 1987). – Forewing length: 6–14 mm. Antennae generally as long as wings or little longer. Maxillary palps 5-segmented, 1st segment short, 2nd segment longer, about twice as long as 1st segment, 3rd and 4th segment shorter than 2nd segment, 5th segment as long as basal four segments, terminal segment with suture-like cross striae. Tibial spurs: 2, 4, 4. Wings similar to those of *Hydropsyche*: in forewing cubitus Cu2 and anal vein 1A are united before wing margin, in hindwing subcosta Sc and radius R_1 are united and run as a single vein to wing margin. Male genitalia: 2-segmented inferior appendages with apical segment as long as, or longer than, basal segment. Basis of phallus is large and bulbous, at apex with a pair of lateral lobes in-between two phallotremal sclerites.

Discussion. – The genus *Calosopsyche* consists of 13 extant species, is distributed in Central-America with five species of the *continentalis*-group, and is spread over the Greater Antilles with eight species of the *calosa*-group (FLINT & BUENO SORIA 1987, FLINT et al. 1999). The *calosa*-group is distinguished from the *continentalis* group by the shape of the apical clasper segment. It is not bifid at the tip or bearing a lobe on one side.

Calosopsyche palaeoelegans n. sp.

Figs. 14a–c, 15

Holotype: Male embedded in Dominican amber; SMNS: Do-820-K.

Paratypes: Two males; one in the amber collection W. WICHARD, Bonn; one in the SMNS: Do-5719.

Etymology: It is an elegant fossil species: *palaeoelegans*.

Diagnosis. – The shape of the apical segment of the inferior appendages classifies *Calosopsyche palaeoelegans* n. sp. to the *calosa*-group. The new species differs from extant species of the *calosa*-group by the extreme curved apical segment of the inferior appendages (Fig. 14c).

Description. – Forewing length: 6.8 mm. General structures and forewing venation typical of the genus (Fig. 14a). Forewing venation essentially as in *Hydropsyche*. Fork I–V present. Discoidal, median, and thyridium cell very probably closed; the cross-veins are not evident in the holotype, but in the paratype. Apex of cubitus Cu2 and anal vein 1A united before wing margin. Hindwing cannot be analysed because it is covered by the forewing.

Male genitalia (Fig. 14c): 10th tergum forms a central membrane, which covers the phallus dorsally. Laterally the central membrane is flanked at both sides by elongated membranes. The apex of the phallus shows the two lateral lobes in-between small dark sclerites. The inferior appendages (claspers) are 2-segmented, basal segment approximately as long as apical segment, the first segments diverge but the second segments draw a bow, with their tips overlapping and touching each other.

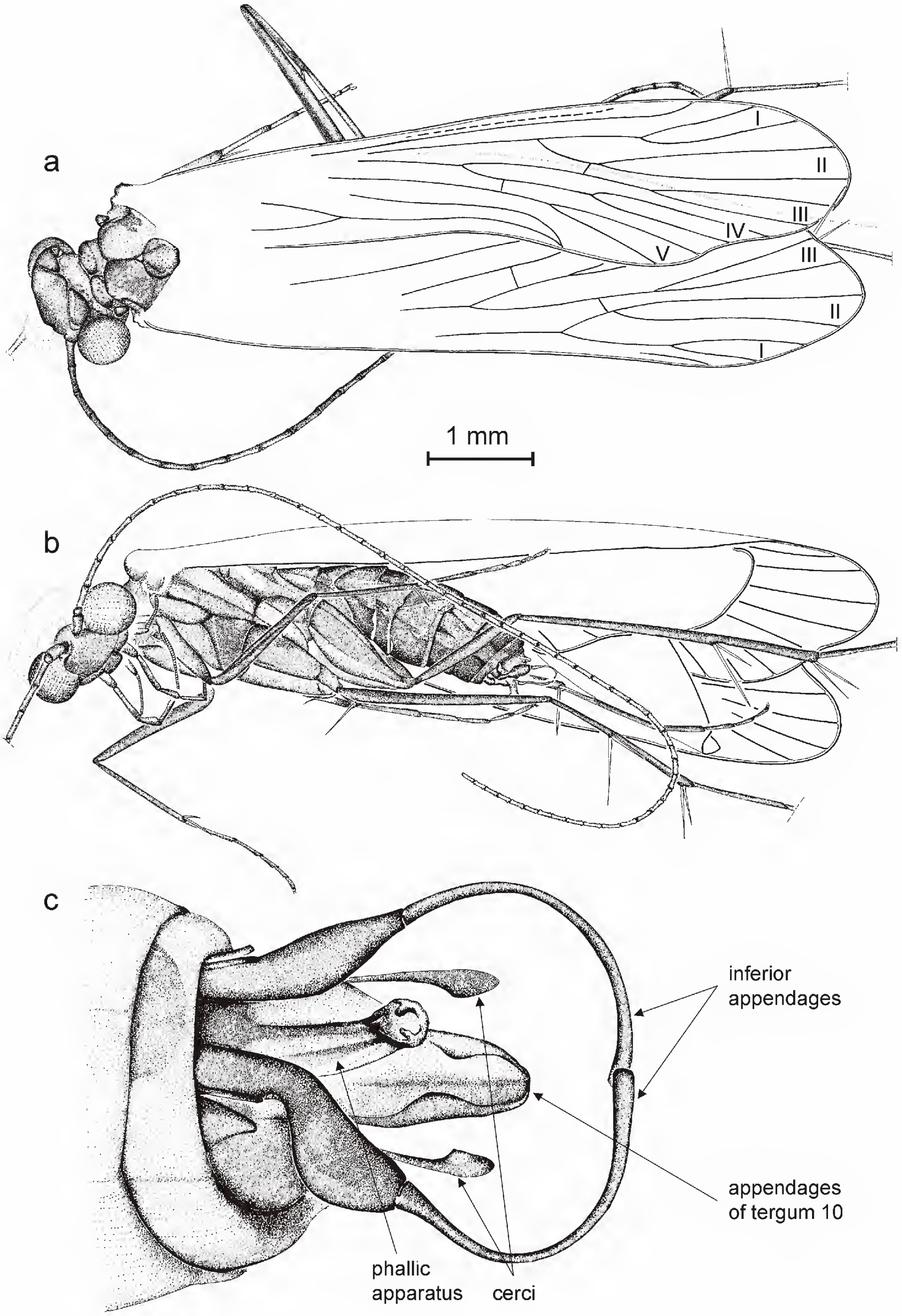
a
I
II
III
IV
V
III
II
I
1 mm
b
c
inferior appendages
appendages of tergum 10
phallic apparatus
cerci

Fig. 14. *Calosopsyche palaeoelegans* n. sp., male, holotype; SMNS: Do-820-K; **a**: dorsal view; **b**: lateroventral view; **c**: genitalia in ventral view.

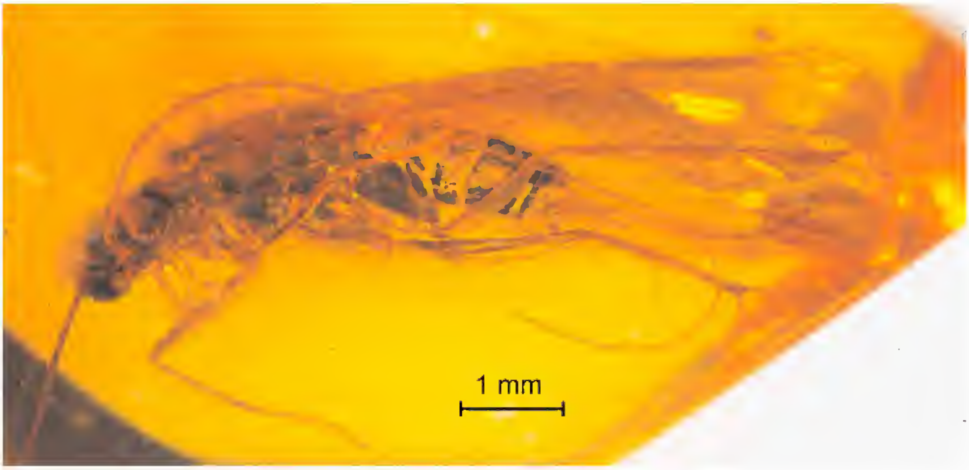

Fig. 15. *Calosopsyche palaeoelegans* n. sp., male in lateroventral view, holotype; SMNS: Do-820-K.

Subfamily Macronematinae Ulmer, 1905
Gattung *Macronema* Pictet, 1836

Type species: *Macronema lineatum* Pictet, 1836

Diagnosis (Flint & Bueno Soria 1982). – Antennae much longer than forewing, maxillar palps 5-segmented, with 3rd segment longer than 2nd segment, 5th terminal segment with suture-like cross striae, much longer than the four basal segments. Tibial spurs: 0, 4, 4 (Neotropical species). In forewing subcosta Sc and vein R_1 are united. Fork I–V present, fork I petiolate. Discoidal cell, median cell, and thyridium cell are closed. Anal veins (1A, 2A, 3A) fused and run as single vein to wing margin. In hindwing discoidal cell is open.

Remarks. – The genus *Macronema* is widely distributed throughout the world (but lacking in Europe), common in the tropic, and present in the Neotropical region with about 30 described species.

Macronema hispaniola n. sp.
Figs. 16a–c, 17

Holotype: Male in Dominican amber; SMNS: Do-2219-K. The holotype is embedded in a small cabochon stone with 1 cm in diameter, face-grinded. Therefore the apical wing-parts as well as the middle and hind legs are truncated.

Paratype: A male in the amber collection W. Wichard, Bonn.

Etymology: It is the first described *Macronema* species from Hispaniola.

Diagnosis. – *Macronema hispaniola* n. sp. is characterized by two genital structures: the triangular shape of lateral lobe-projections of the 9th segment and the apical thin spicules of the phallus forming a ring.

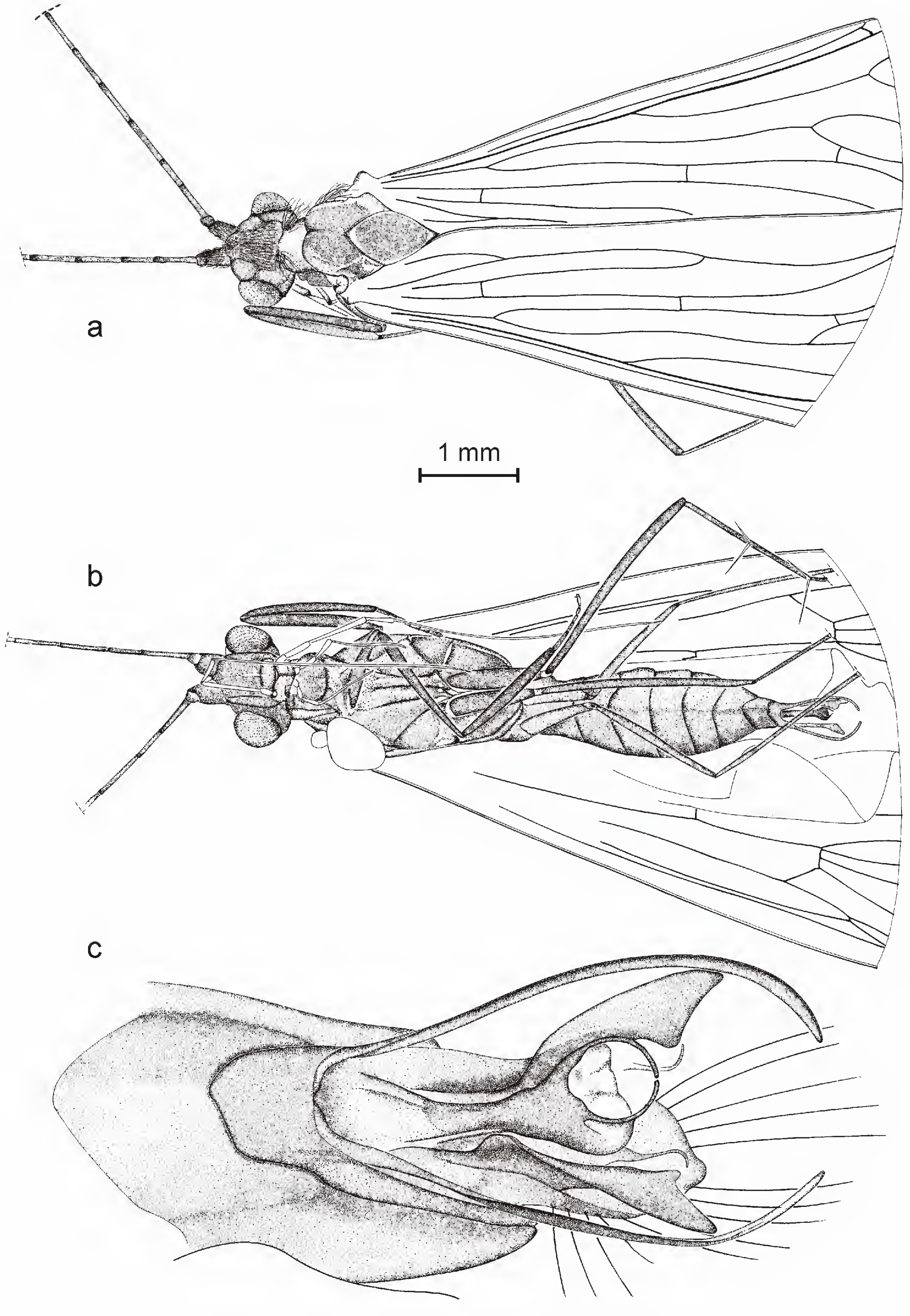

Fig. 16. *Macronema hispaniola* n. sp., male, holotype; SMNS: Do-2219-K; **a**: dorsal view; **b**: ventral view; **c**: genitalia in ventral view.

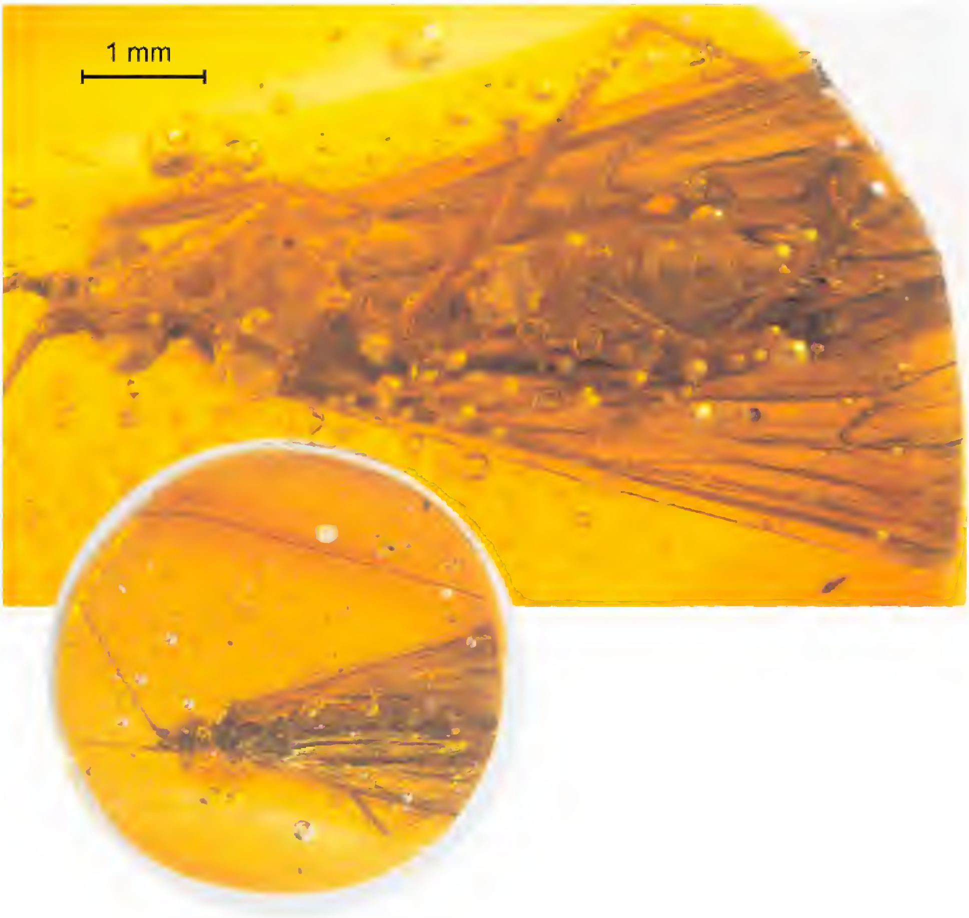

Fig. 17. *Macronema hispaniola* n. sp., male in ventral view, holotype; SMNS: Do-2219-K; inset: holotype in dorsal view embedded in a round cabochon stone with 1 cm in diameter.

Description. – Forewing length: 8.6 mm (paratype). General structures and wing venation of *Macronema*. In forewing subcosta Sc and radius R_1 are united and run as a short single vein – after study of the paratype – to the costa (apical wing margin). On the level of vein fusing Sc and R_1 a crossvein is connected to the costa additionally. (The apical venation of Sc and R_1 allows another interpretation: Subcosta Sc and radius R_1 run parallelly without fusion and a crossvein connecting Sc and R_1 at the level of ending Sc in wing margin.) In paratype forewing the discoidal cell is diminutive, the median cell normal in size, and the thyridium cell is long and slender.

The male genitalia (Fig. 16c): The slender inferior appendages (claspers) seem to be single-jointed, both drawing together an elongated bow which is open distal. In their middle the phallic apparatus is placed and constructed shortly, stoutly and compactly. At the apex the phallus is opened like a funnel and possesses ventrally two thin spicules forming a ring, distal nearly closed. Dorsolaterally the phallic apparatus is flanked at both sides by lobes of 9th segment (cerci?) constructing triangular projections. The male genitalia are covered dorsally by the hood of the 10th segment.

Discussion. – This new species is the first fossil *Macronema* and the first described species of Hispaniola. FLINT & SYKORA (2004) mentioned undetermined larvae found in Haiti by L. BOTOSANEANU. Nevertheless, from Greater Antilles three extant species are known: *M. tremenda* BOTOSANEANU, 1980 (Cuba), *M. matthewsi* FLINT, 1964 (Puerto Rico), and *M. gundlachi* BANKS, 1924 (Cuba). Probably the extant as well as the fossil new species from the Greater Antilles are closely related and belong to the *lineatum*-group. Common characteristics are the diminuitive discoidal cells and the crossvein connecting the costa at the level of the $Sc + R_1$ vein fusing.

Family Ecnomidae ULMER, 1903
Genus *Austrotinodes* SCHMID, 1955

Type species: *Austrotinodes latior* SCHMID, 1955

Diagnosis (FLINT 1973). – Forewing length: 6–8 mm (extant species), ocelli absent. Maxillary palps with terminal segment elongate and with suture-like cross striae. Mesoscutum and mesoscutellum, each bears a pair of small setose warts. Tibial spurs formula: 3, 4, 4. Forewing radius R_1 is subdivided apically into two branches. Apical fork II ($R_4 + R_5$), III ($M_1 + M_2$), IV ($M_3 + M_4$), V (Cu1a + Cu1b) present; apical fork I ($R_2 + R_3$) is absent, discoidal, median, and thyridium cells present.

Remarks. – The genus *Austrotinodes* is widely distributed in the Neotropics and was found in Mexico, Ecuador, and Puerto Rico as well as in Chile, Brazil, and Argentina and in other South American countries (FLINT et al. 1999). However, only few species are known from the Lesser and Greater Antilles. So far, it is *Austrotinodes cubana* KUMANSKI, 1987 from Cuba and *Austrotinodes madininae* BOTOSANEANU, 1990, a described female from Martinique. An undescribed female is mentioned from the Dominican Republic (BOTOSANEANU 1990).

Austrotinodes sp.
Fig. 18

Material: Female found in Dominican amber; SMNS: Do-4143-M.

Description. – Length of forewing: 4.1 mm. General structure and forewing venation typical of genus, discoidal, median, and thyridium cells closed, but the apical crossveins of all three cells indistinct. Female genitalia (ventrally covered by the right leg, dorsally by the wings) with 9th segment strongly prolonged in a straight tube, 10th segment elongate and (from lateral view of the embedded fossil) terminally with two pairs of three small papillae, one of the three papillae longer than the other two.

Discussion. – The very narrow structures of female genitalia and the conformity of the wing venation in *Austrotinodes* do not allow new species descriptions; hence the female of the genus *Austrotinodes* is not further described and remains unnamed. Due to the similarity of females and a lack of allocation to the corresponding males, new Trichoptera species from amber are described according to the more differentiated outer genital structures of the males.

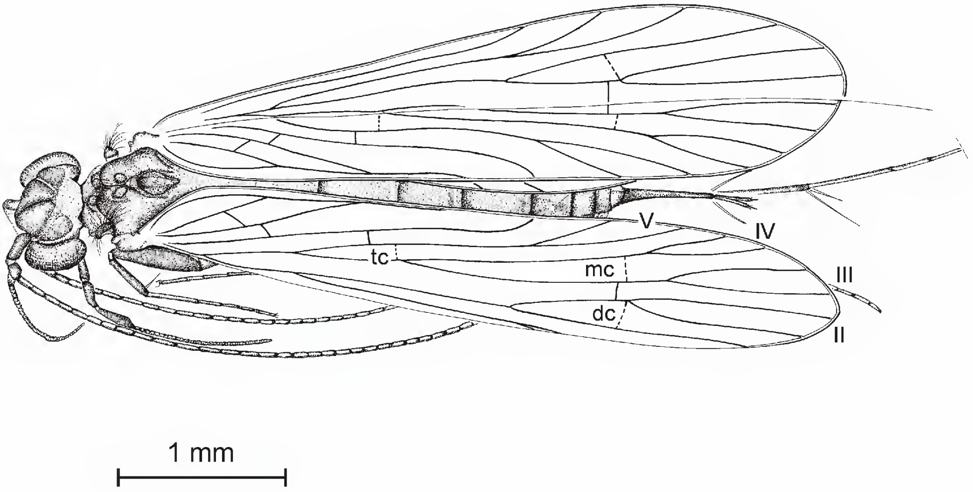

Fig. 18. *Austrotinodes* sp., female in dorsal view; SMNS: Do-4143-M.

Family Dipseudopsidae Ulmer, 1904
Subfamily Pseudoneureclipsinae Ulmer, 1951
Genus *Antillopsyche* Banks, 1941

Type species: *Antillopsyche wrighti* Banks, 1941

Diagnosis. – The adults of *Antillopsyche* without ocelli, maxillary palps with terminal segment, elongated and with suture-like cross striae, mesoscutum bears a pair of setose warts; forewing with apical fork I–V; discoidal, median, and thyridium cells closed; tibial spurs: 3, 4, 4. *Antillopsyche* is characterized by the hindwing venation (apomorphy): apical fork II, III, and V present, the discoidal cell is open.

Remarks. – Almost half of all Dominican amber caddisflies belong to the genus *Antillopsyche*, in particular to *A. oliveri* and *A. auricula*. Three fossil species were identified in Dominican amber and a further one was detected in Mexican amber (Wichard et al. 2006). Four extant species (*A. aycara* Botosaneanu, 1980, *A. demma* Botosaneanu, 1996, *A. tubicola* Flint, 1964, and *A. wrighti* Banks, 1941) are endemic in the isles of the Great Antilles, on Cuba, on Hispaniola, and on Puerto Rico (Flint et al. 1999). *Antillopsyche* is closely related to the genus *Pseudoneureclipsis*, which is rich in species and primarily represented in the Old World tropics. Within the family Dipseudopsidae the two genera form the subfamily Pseudoneureclipsinae.

It is imaginable that *Antillopsyche* could spread through the Great Antilles during the Mesozoic period, when South America and Africa were closely connected with each other and the subfamily Pseudoneureclipsinae could spread from Ethiopian and Oriental regions to the Neotropics. The absence of *Antillopsyche* in North America indicates that the distribution towards America took only place in the Jurassic, when North America was detached from South America. *Antillopsyche* was also found in Mexican amber of Chiapas, which has approximately the same geological age as the Dominican amber. Consequently it is supposed that a distribution of this genus must have taken place at least in the Miocene.

Key to fossil *Antillopsyche* species

1 Elongated cerci of 9th tergum overtop the level of the genitalia .... ***oliveri***
– Cerci of 9th tergum do not overtop the level of the genitalia 2
2 Digitiform shape of the cerci of 9th segment .... ***digitus* n. sp.**
– Auriculate shape of the cerci of 9th segment 3
3 Shape of the lobes of 10th tergum flat and wide .... ***auricula* n. sp.**
– Shape of the lobes of 10th tergum small and diverged .... ***mexicana***

Antillopsyche oliveri Wichard, 1985

Figs. 19a–d

Holotype: Male embedded in Dominican amber; SMNS: Do-5708 (ex Coll. Wichard).

Paratypes: Seven males embedded in Dominican amber: Two in the amber collection of the SMNS: Do-819-K-1, Do-2720-D-1; four in the amber collection W. Wichard, Bonn; one in the amber collection of the NMNH.

Diagnosis. – *Antillopsyche oliveri* differs from all recent and from the fossil species *A. auricula* n. sp. and *A. digitus* n. sp. in the male genitalia. The species is characterized by the long and small cerci of the 9th tergum and in dorsal view by the mesal parallel bands or skewers of 10th tergum, which taper towards periphery.

Description. – *Antillopsyche oliveri* is refigured and described for completeness and for comparison with the new species *Antillopsyche auricula* n. sp. and *A. digitus* n. sp.

Length of forewing: 4.3 mm (holotype). General structure, forewing, and hindwing venation typical of the genus (Figs. 19a–b). Male genitalia (Figs. 19c–d): Tergum of 9th segment with long cerci, protruding far about the apical level of the genitalia, in lateral view fingerlike, in ventral view small and slightly twisted. Tergum of 10th segment with two mesal membranous parallel lobes, apical margins tapering towards periphery. Clasper, apical rounded, margin slightly tubercular, with a basodorsal appendage, which bents mesad. Aedeagus jacketed by laterodorsal membrane, membranous apex not covered with a cluster of spines.

Antillopsyche auricula n. sp.

Figs. 20a–c, 21

Holotype: Male embedded in Dominican amber; SMNS: Do-5714 (ex Coll. Wichard).

Paratypes: Two males, one in the amber collection W. Wichard, Bonn; one in the amber collection of AMNH: DR-14-833.

Etymology: Named to the auriculate shape of the cerci of 9th segment.

Diagnosis. – *Antillopsyche auricula* n. sp. is closely related to the fossil *A. mexicana* Wichard et al., 2006. Cerci and claspers are similar in appearance, but both species differ in the shape of the lobes of 10th tergum. In *A. auricula* n. sp. the lobes are flat and wide, whereas the lobes of *A. mexicana* are smaller and diverged.

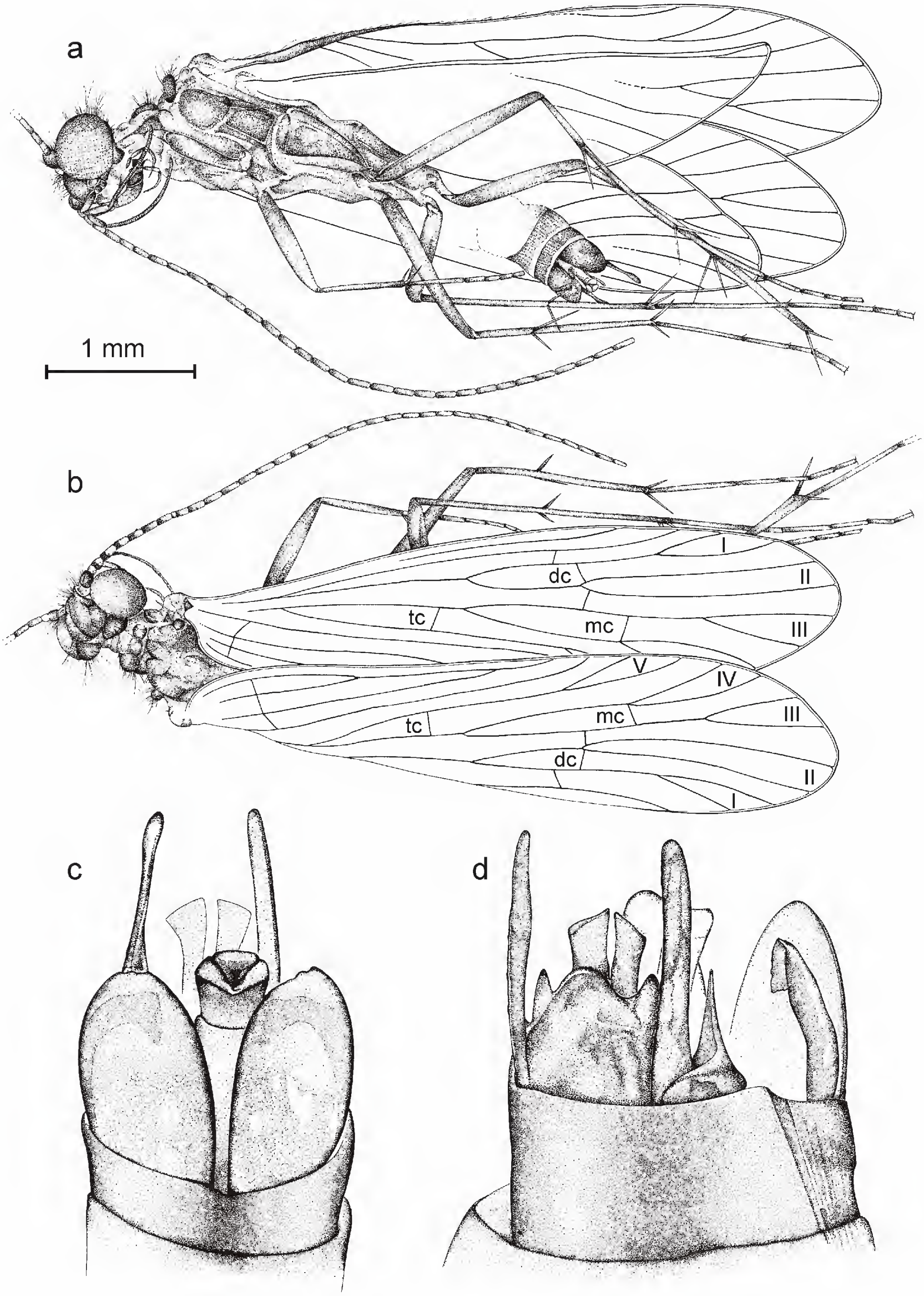
a
1 mm
b
I
dc
II
tc
mc
III
V
IV
tc
mc
III
dc
II
I
c
d

Fig. 19. *Antillopsyche oliveri* Wichard, 1985, male, holotype; SMNS: Do-5708 (ex Coll. Wichard); **a**: ventrolateral view; **b**: dorsal view; **c**: genitalia in ventral view; **d**: genitalia in dorsolateral view.

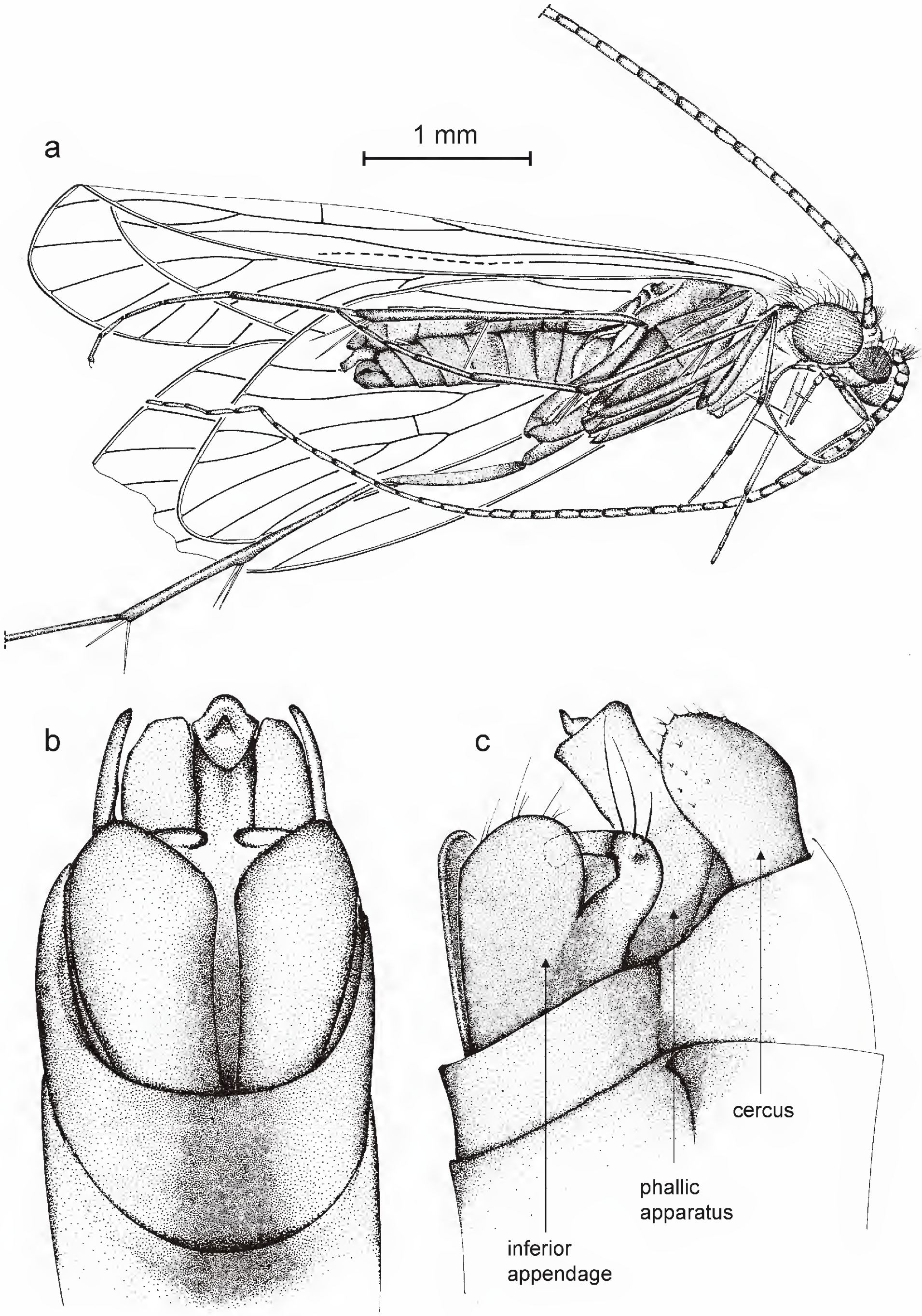
a
1 mm
b
c
cercus
phallic apparatus
inferior appendage

Fig. 20. *Antillopsyche auricula* n. sp., male, holotype; SMNS: Do-5714 (ex Coll. WICHARD); **a**: ventrolateral view; **b**: genitalia in ventral view; **c**: genitalia in lateral view.

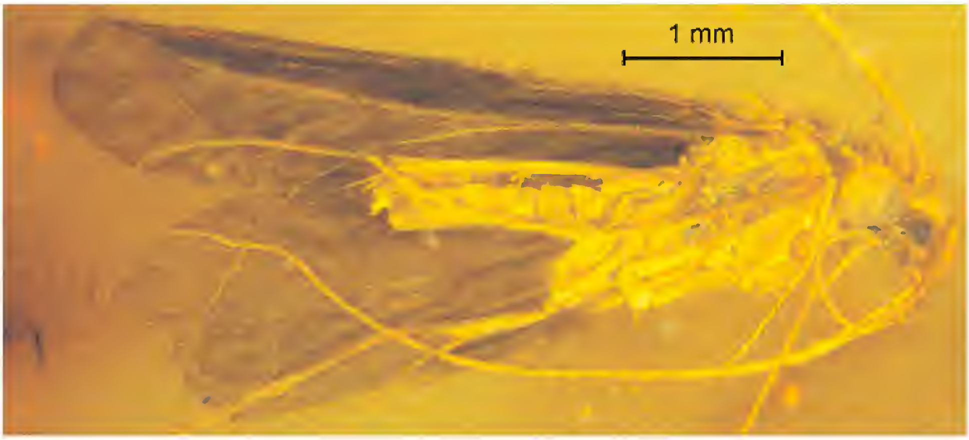

Fig. 21. *Antillopsyche auricula* n. sp., male in ventrolateral view, holotype; SMNS: Do-5714 (ex Coll. Wichard).

Description. – Length of forewings: 4.2–5.0 mm. General structure as well as fore- and hindwing venation typical of the genus. Male genitalia (Figs. 20b–c): Tergum of 9th segment with auriculate cerci in lateral view, but in ventral view very small, on a level with the flat lobes of 10th tergum. In ventral view one can see the wide and flat lobes between the small cerci, in the middle ventral the phallic apparatus is visible. In ventral and lateral view the pair of claspers, long and oval, apical margin slightly tapered mesad, with a basodorsal appendage, which bents mesad.

Antillopsyche digitus n. sp.

Figs. 22a–c, 23

Holotype: Male embedded in Dominican amber; SMNS: Do-5715 (ex Coll. Wichard).
Etymology: Digitus = finger: named to the finger-like shape of the cerci of 9th segment.

Diagnosis. – *Antillopsyche digitus* n. sp. is closely related to the fossil *A. oliveri.* Lobes of 10th tergum, cerci and claspers are similar in appearance, but in *A. digitus* n. sp. the parallel lobes are apically rounded instead of tapered towards periphery, the digitiform cerci do not overtop the level of the genitalia, and the margins of the claspers are more distinct than in *A. oliveri.*

Description. – Length of forewings: 4.8 mm. General structure and fore- and hindwing venation typical of the genus. Male genitalia (Figs. 22b–c): Tergum of 10th segment with two mesal membranous parallel lobes, apical margins rounded. Tergum of 9th segment with digitiform cerci in lateral view, in ventral view smaller, on a level with the claspers. In ventral view a pair of claspers, long and slightly curving dorsad and mesad, the straight margin is rounded and apikomesal concaved, basodorsal with an appendage, which bents mesad and is acuminated with one or probably two tips.

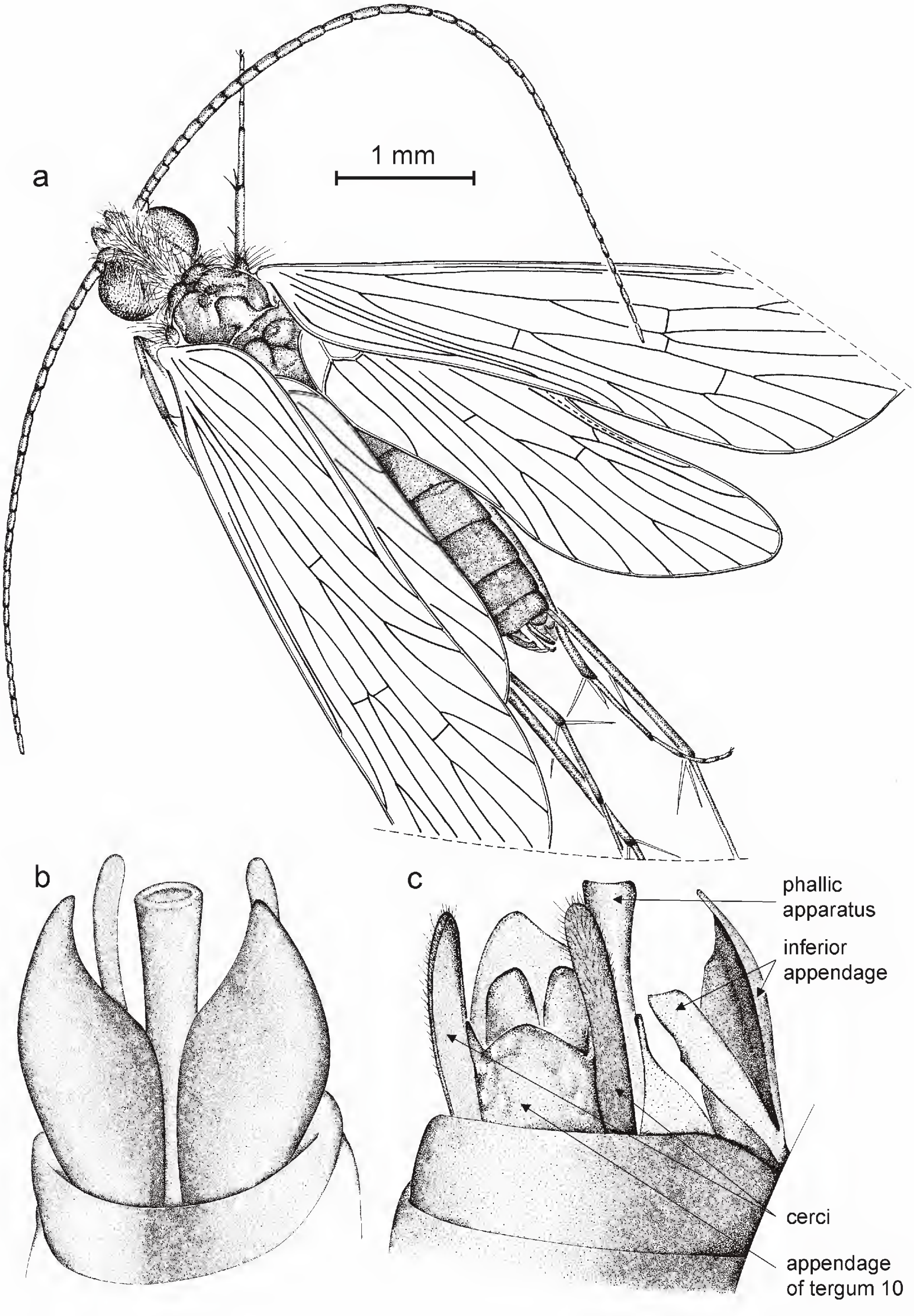
a
1 mm
b
c
phallic apparatus
inferior appendage
cerci
appendage of tergum 10

Fig. 22. *Antillopsyche digitus* n. sp., male, holotype; SMNS: Do-5715 (ex Coll. WICHARD); **a**: dorsal view; **b**: genitalia in ventral view; **c**: genitalia in dorsolateral view.

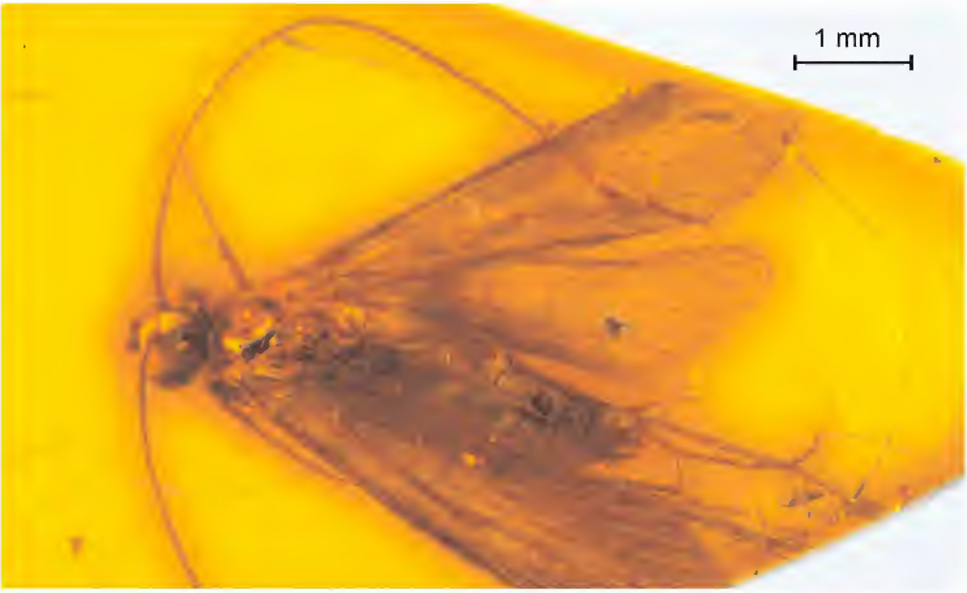

Fig. 23. *Antillopsyche digitus* n. sp., male in dorsal view, holotype; SMNS: Do-5715 (ex Coll. WICHARD).

Family Polycentropodidae ULMER, 1903
Genus *Cernotina* ROSS, 1938

Type species: *Cernotina calcea* ROSS, 1938

Diagnosis. – The adults of genus *Cernotina* are characterized by the absence of ocelli, by the presence of the 5-segmented maxillary palps: terminal segment elongated and with suture-like cross striae, second segment small and with the apex enlarged into a small lateral cushion. The mesoscutum bearing a pair of distinct setal warts. Forewing venation with fork II ($R_4 + R_5$), IV ($M_3 + M_4$), and V (Cu1 branched), discoidal and thyridium cells closed. Tibial spurs: 2, 4, 4.

Remarks. – The genus *Cernotina* is distributed in the New World, from North and Central America southwards to Rio de la Plata. It is known from Greater and Lesser Antilles (FLINT & SYKORA 2004). Nevertheless, from more than 50 Neotropical species less than eight species are found in Central America and the Antilles (FLINT et al. 1999).

Cernotina pulchra n. sp.
Figs. 24a–c, 25

Holotype: Male embedded in Dominican amber; SMNS: Do-5716 (ex Coll. WICHARD).

Paratype: Male embedded in Dominican amber, kept in the amber collection W. WICHARD, Bonn.

Etymology: Pulchra = beautiful: beautifully embedded in Dominican amber.

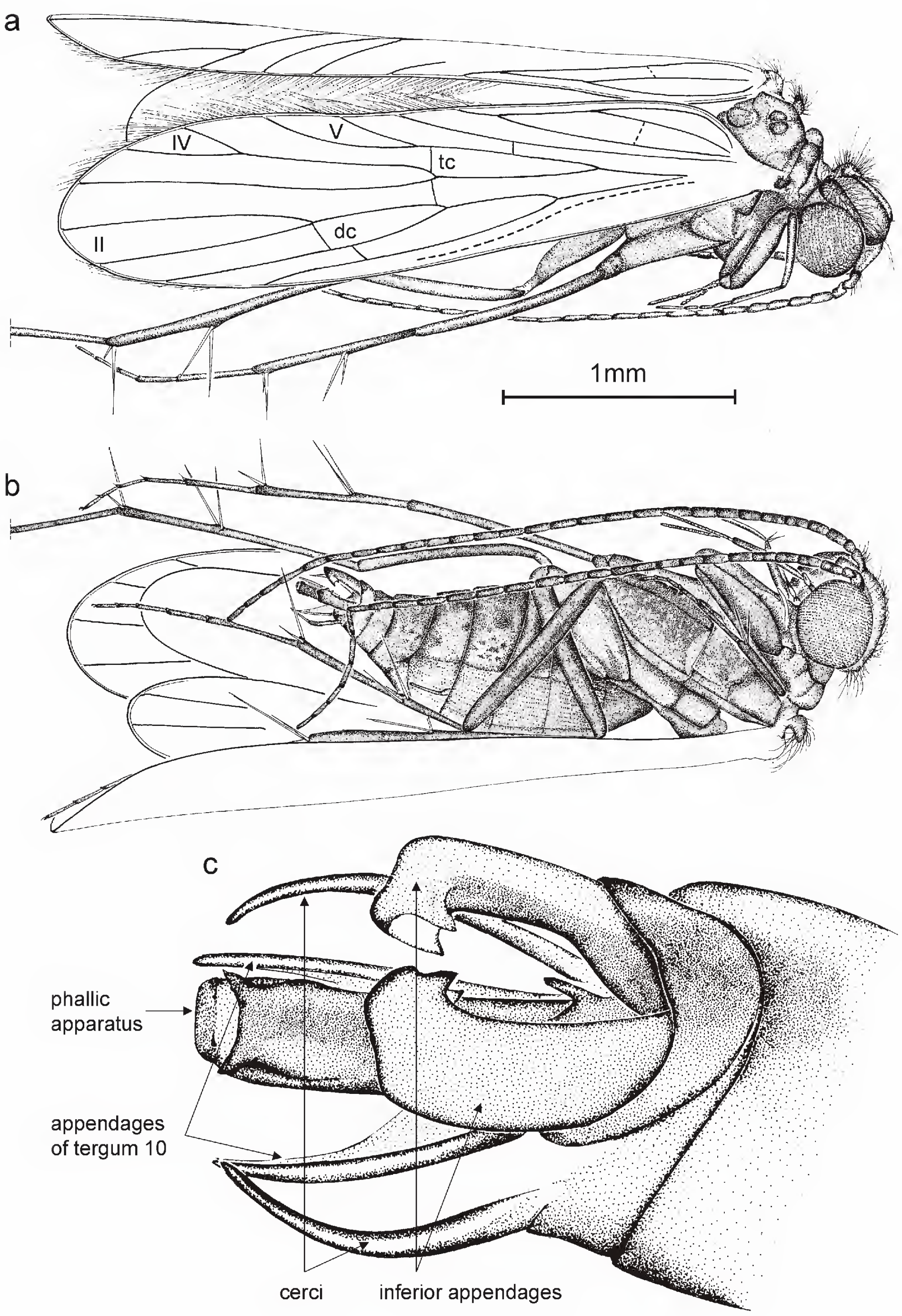
a
IV
V
tc
II
dc
1mm
b
c
phallic apparatus
appendages of tergum 10
cerci
inferior appendages

Fig. 24. *Cernotina pulchra* n. sp., male, holotype; SMNS: Do-5716 (ex Coll. WICHARD); **a**: dorsolateral view; **b**: ventrolateral view; **c**: genitalia in ventrolateral view.

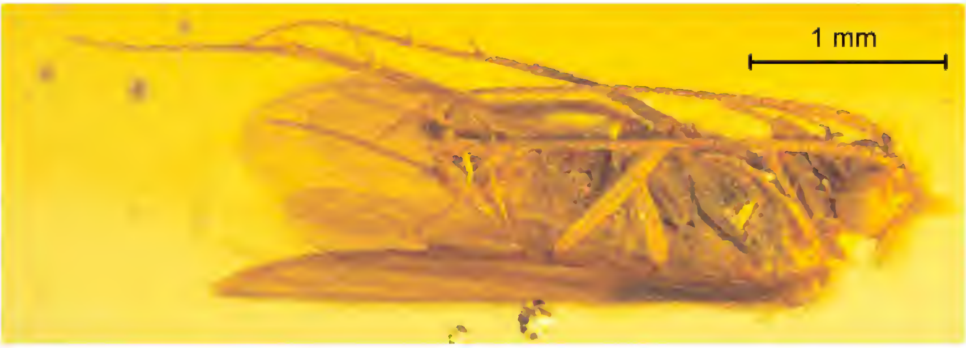

Fig. 25. *Cernotina pulchra* n. sp., male in ventrolateral view, holotype; SMNS: Do-5716 (ex Coll. Wichard).

Diagnosis. – First fossil *Cernotina*, presumably closely related to *C. danieli* Flint & Sykora, 2004 (type location: Dominican Republic), and especially to *C. caliginosa* Flint, 1968 (type location: Jamaica). They all correspond in the shape of the inferior appendages but in *Cernotina pulchra* n. sp. without blackened hook apicodorsally and without a dorsomesal row of small spinose setae. *C. pulchra* n. sp. corresponds with *C. caliginosa* Flint, 1968 in the shape of the semimembranous 10th tergum, consisting of trianguloid lobes at each side of aedeagus. The cercus of the new species is an elongated spine as long as the dorsal processes of 10th tergum curved slightly mesad (Fig. 24c).

Description. – Length of forewing: 2.8–3.2 mm. General structure and forewing venation typical of the genus (Figs. 24a–b). Male genitalia (Fig. 24c): 10th tergum divided dorsomesally with two elongated processes, both laterally enlarged by triangular sail membranes which touch dorsomesally at basal triangular edges. The thin membranes are slightly transparent in the paratype, whereas in the holotype the membranes are non-transparent. Lateral from both sides of the genitalia an elongated cercus is present, which is as long as the dorsal processes of the 10th tergum curved slightly mesad. The apical tips of these lateral processes are darkened. Inferior appendages of 9th sternum are elongated, rectangularly rounded, and curved ventromesad. The apex of the inferior appendages is divided into a ventromesal and a dorsomesal membranous lobe. Aedeagus probably with narrow long lateral sclerites.

Suborder Integripalpia Martynov, 1924
Family Calamoceratidae Ulmer, 1905
Genus *Phylloicus* Mueller, 1880

Type species: *Phylloicus major* Mueller, 1880

Diagnosis (Prather 2003). – Length of forewing: 7.0–18.5 mm. Mesoscutum and mesoscutellum without distinct warts. Tibial spurs formula: 2, 4, 4 or 2, 4, 3 or 2, 4, 2. In the forewing apical fork I–V present, discoidal and medial cells closed, radius R_1 recurrent onto radius R_2 or free to wing margin. In hindwing apical fork II, III, and V present, discoidal and median cells open. Male genitalia: Inferior appendages (claspers) are 2-segmented: the basal coxopodite and the small harpago cylindrical or tapered apically, bearing short, pointed, peglike setae. Preanal appendages (cerci) are varying in length and shape, bearing most setae. 10th tergum most often distinctly separated and varying in shape, often with digitate process arising basomesally. Phallobase a simple curved tube, at apex the everted endotheca consists of multiple membranous lobes with species-specific arrangement.

Phylloicus velteni n. sp.

Figs. 26a–c, 27

Holotype: Male embedded in Dominican amber; SMNS: Do-5717.

Etymology: Dedicated to JÜRGEN VELTEN, who offered the Dominican amber with the inclusion of the new caddisfly for our analysis and donated it to the amber collection of the SMNS.

Diagnosis. – *Phylloicus velteni* n. sp. belongs to the group of species of predominantly Antillean distribution (PRATHER 2003). They are characterized by tibial spurs 2, 4, 2 and a long digitate basodorsal process of 10th male tergum. Four of six extant species have bright orange (*P. cubanus* BANKS, 1924, *P. iridescens* BANKS, 1941, *P. pulchrus* FLINT, 1964, and *P. superbus* BANKS, 1938) or white (*P. amazonas* PRATHER, 2003) forewing bands. But *P. chalybeus* (HAGEN, 1861) and *P. velteni* n. sp. lack forewing ornamentation. *P. velteni* n. sp. differs from *P. chalybeus* and from all other species of this group by the deeply cleft 10th tergum which is divided into two long lateral processes.

Description. – Length of forewing: 8.5 mm. General structure and forewing venation typical of genus (fork I–V present, discoidal and medial cells closed), but radius R_1 recurrent onto R_2, forewings seem to be without any ornamentation (Fig. 26a). Tibial spurs formula: 2, 4, 2. Male genitalia (Fig. 26c): Both inferior appendages consist of a dominant coxopodite and a smaller harpago that are tapered apically and bearing some short peglike setae at the tips. The preanal appendages are elongated, bearing a lot of long setae. In lateroventral view, 10th tergum is deeply cleft and divided into two long lateral processes, additionally with long digitate basodorsal process; the tree processes approximately equal in length to preanal appendages.

Family Helicopsychidae ULMER, 1906

Genus *Helicopsyche* VON SIEBOLD, 1856

Type species: *Helicopsyche shuttleworthi* VON SIEBOLD, 1856

Diagnosis (JOHANSON 1995, 1998). – Antennae as long as the forewings or longer. Scapus about three to five times longer than pedicellus. Maxillary palps 2-segmented. Cephalic and postantennal warts well developed. Pronotum with two pairs of setal warts, mesonotum and mesoscutellum with one pair of setal warts. Tibial spurs formula: (1) 2, 2, 4 or 1, 2, 2; the anterior spur always shorter than the pos-

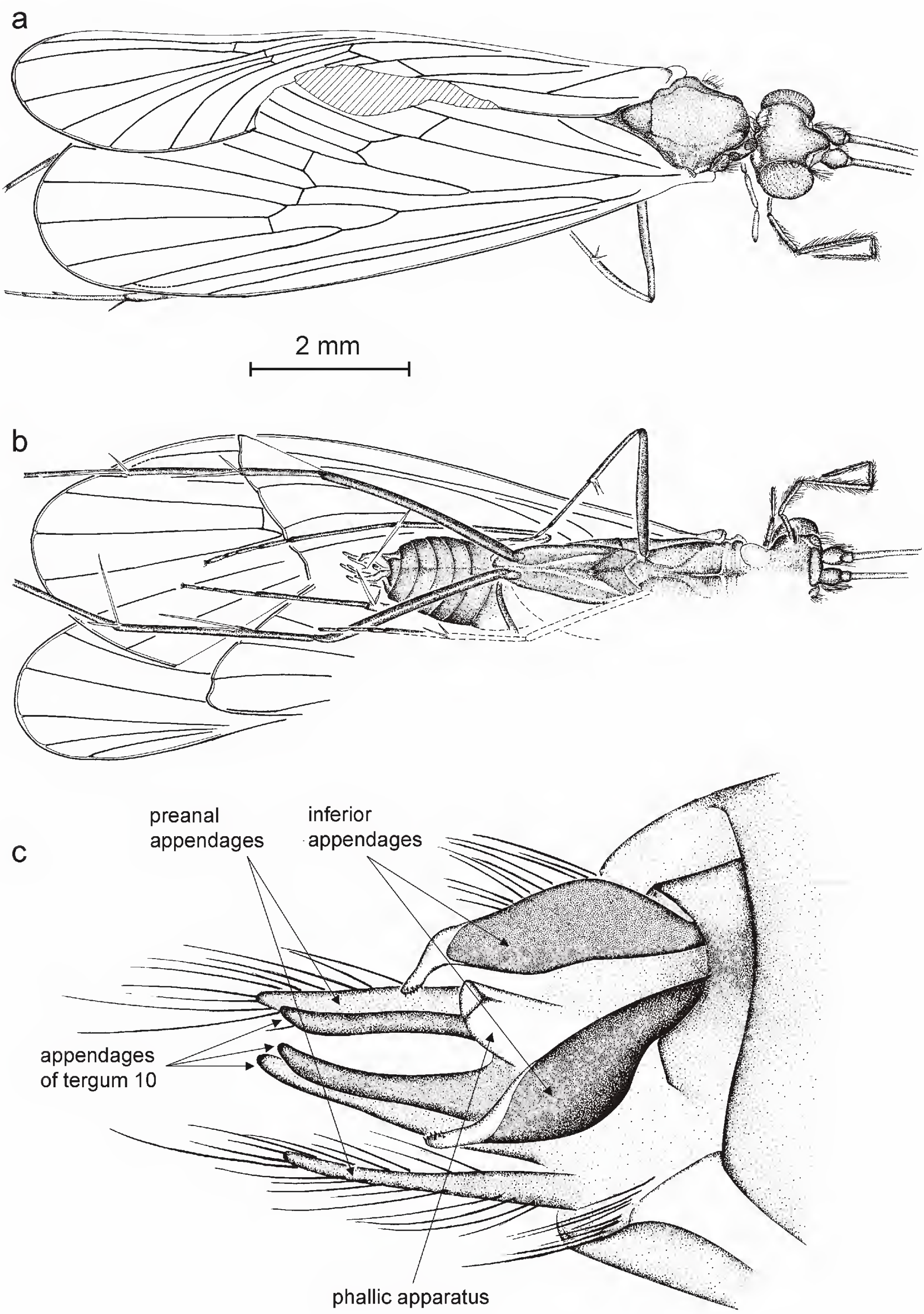
a
2 mm
b
c
preanal appendages
inferior appendages
appendages of tergum 10
phallic apparatus

Fig. 26. *Phylloicus velteni* n. sp., male, holotype; SMNS: Do-5717 (ex Coll. VELTEN); **a**: dorsal view; **b**: ventral view; **c**: genitalia in ventrolateral view.

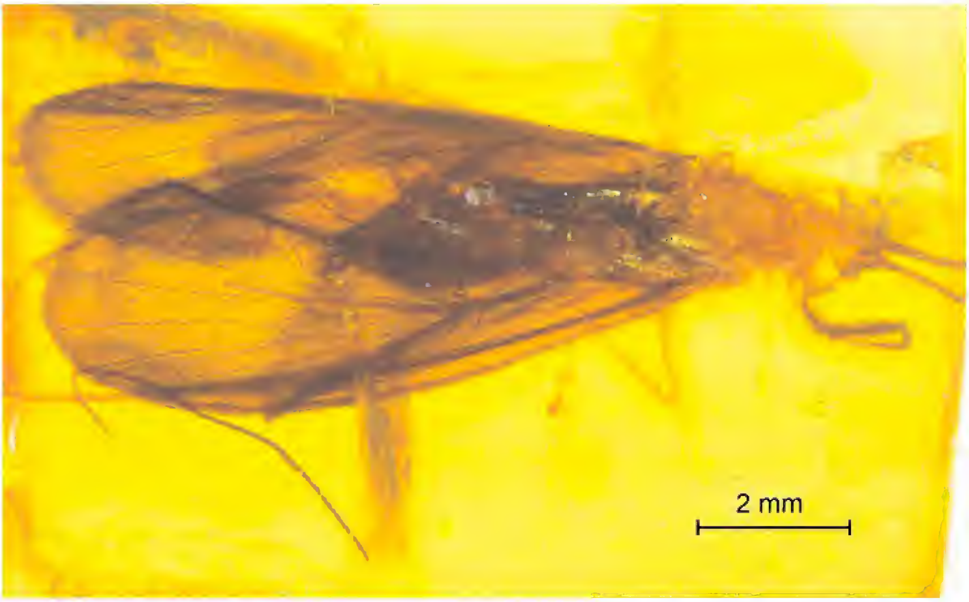

Fig. 27. *Phylloicus velteni* n. sp., male in dorsal view, holotype; SMNS: Do-5717 (ex Coll. VELTEN).

terior spur, or absent. Forewings with closed discoidal cells. Fork I (R_2 + R_3) and fork II (R_4 + R_5) present. M_1 + M_2 present (fork III) or fused (M_{1+2}), M_3 + M_4 fused (M_{3+4}). Cubitus Cu1 divides into Cu1a and Cu1b (fork V), Cubitus Cu2 well developed. Hindwings with well developed, curved hamuli, anterior margin sigmoid. R_2 + R_3 separate (fork I present) or fused (R_{2+3}), fused R_{4+5} present. M_1 + M_2 separate (fork III present) or fused (M_{1+2}), fused M_{3+4} present. Cubitus Cu2 well developed and separate from Cu1. Anal veins diverging. Nygma is absent in all wings. 6th sternal process present in most species.

Subgenus *Feropsyche* JOHANSON, 1998

Type species: *Notidobia borealis* HAGEN, 1861

Diagnosis (JOHANSON 1998). – American *Helicopsyche* belong to the subgenus *Cochliopsyche* or to the largest subgenus *Feropsyche*. In *Feropsyche* the antennae are less than twice the length of the forewing, whereas in *Cochliopsyche* the very thin antennae are more than twice the length of the forewing. The hind tibiae possess 2 preapical spurs in *Feropsyche* but *Cochliopsyche* does not possess preapical spurs in hind tibiae (JOHANSON 1998).

Remarks. – In Dominican amber three species are found and described: *H. scaloida*, *H. voigti*, *H. electra*. All three species belong to the newly established subgenus *Feropsyche* because the tibia spur number is 2, 2, 4 with 2 preapical spurs in hindtibia. Antenna length is another important diagnostic trait to distinguish between the subgenera *Feropsyche* and *Cochliopsyche*. However, for amber specimens it cannot be determined because the antennae are truncated and shortened.

A redescription of three species follows. The revision is necessary after a new careful preparation of the amber specimens and is based on wing structure, which could not be examined prior to the detailed preparation procedure.

Key to fossil *Helicopsyche (Feropsyche)* species

1 Gonopod without ventrobasal branches, forewing with fork I, II, V .... *electra*
– Gonopod with basomedian branch 2
2 Gonopod with basomedian branch elongated like a stylus, forewing with fork I, II, V ... . *scaloida*
– Gonopod with basomedian branch like a short thump, forewing with fork I, II, III, V ... . *voigti*

Helicopsyche (Feropsyche) scaloida JOHANSON & WICHARD, 1996
Figs. 28a–d, 29

Holotype: Male embedded in Dominican amber (Figs. 28c–d, 29); GPIMH: Typ. No. 3751.

Paratype: Male embedded in Dominican amber; SMNS: Do-5720 (ex Coll. WICHARD).

Material: A further specimen (Figs. 28a–b) is kept in the amber collection W. WICHARD, Bonn.

Diagnosis. – In forewing fork I ($R_2 + R_3$) and fork II ($R_4 + R_5$) present; bifurcation of R_{2+3} in $R_2 + R_3$ originates laterally on the discoidal cell; discoidal cell closed; bifurcation of R_{4+5} in $R_4 + R_5$ originates at distal crossvein of the discoidal cell; media M divided distally in M_{1+2} and M_{3+4}; fork III and IV are absent. (Fork III is present, if M_{3+4} is fused with crossvein M-Cu1 plus a last distal sector of Cu1 plus Cu1a.) The thyridium cell is closed and twice as long as the discoidal cell. Cubitus Cu1 distally divided in Cu1a and Cu1b; fork V is present; Cubitus Cu2 ending in Cu1b. In hindwing fork I ($R_2 + R_3$) is absent, discoidal cell open, and fork III ($M_1 + M_2$) probably present. Forewing length: 6.0–7.8 mm.

Male genitalia represented in Figs. 28c–d and described in JOHANSON & WICHARD (1996).

Helicopsyche (Feropsyche) electra JOHANSON & WICHARD, 1996
Figs. 30a–d

Holotype: Male embedded in Dominican amber; SMNS: Do-5698 (ex Coll. WICHARD).

Diagnosis. – In forewing (Fig. 30a) fork I ($R_2 + R_3$) and fork II ($R_4 + R_5$) present; bifurcation of radius R_{2+3} in $R_2 + R_3$ originates laterally on the discoidal cell; discoidal cell closed; bifurcation of radius R_{4+5} in $R_4 + R_5$ originates at distal crossvein of the discoidal cell. Radius R_5 fused with a short medial sector of M_{1+2}. Media M divides in M_{1+2} and M_{3+4}; fork II and IV absent. The thyridium cell is closed and nearly twice as long as the discoidal cell. Distal crossvein of the thyridium cell nearby the

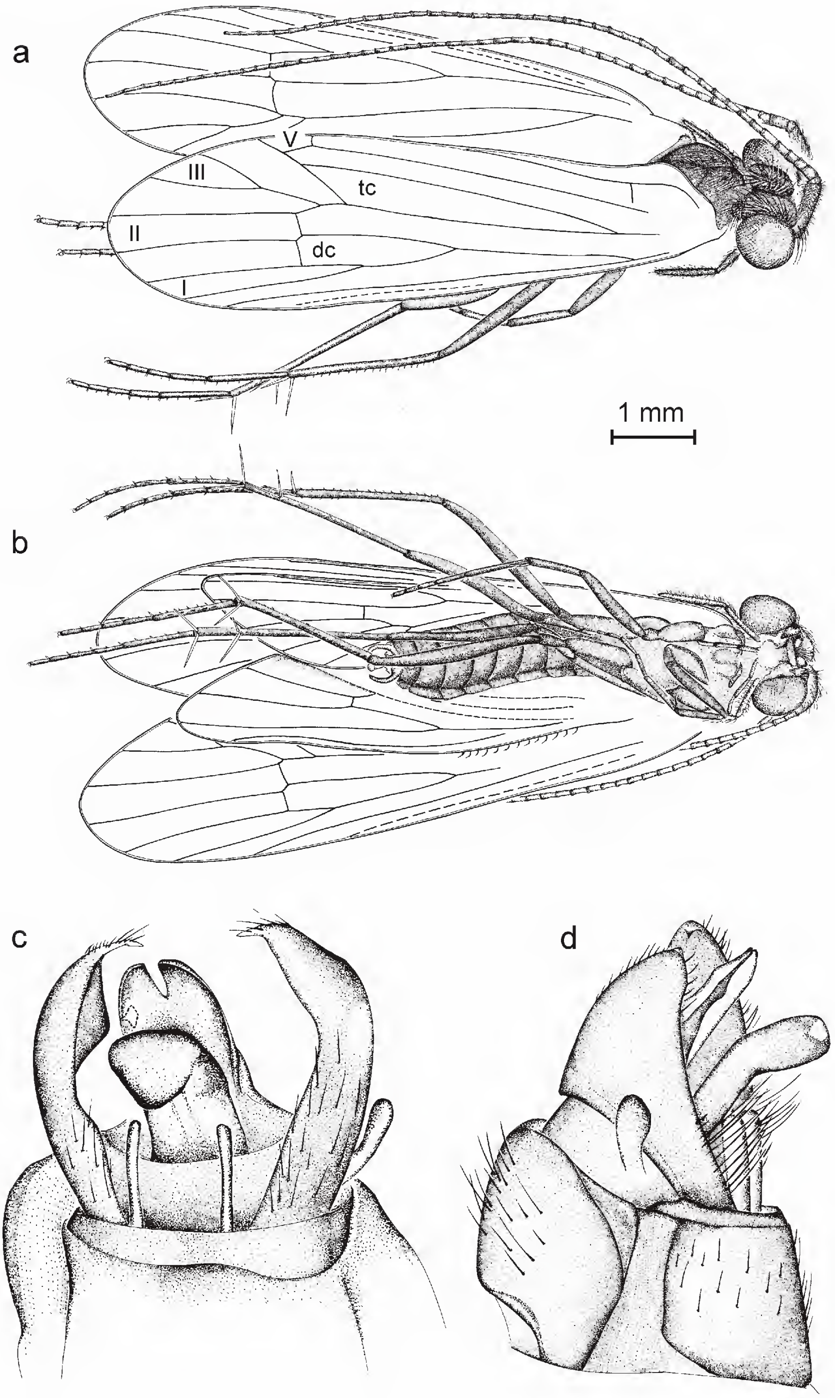

Fig. 28. *Helicopsyche (Feropsyche) scaloida* Johanson & Wichard, 1996, males; **a–b**: Coll. Wichard; **a**: dorsal view; **b**: ventral view; **c–d**: holotype, GPIMH: 3751; **c**: genitalia in ventral view; **d**: genitalia in lateral view.

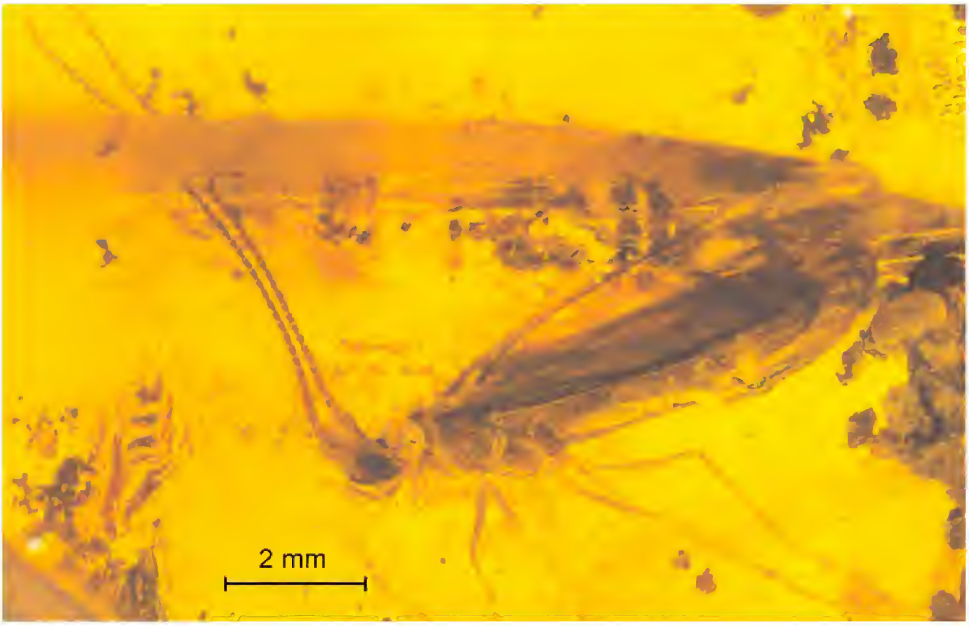

Fig. 29. *Helicopsyche (Feropsyche) scaloida* JOHANSON & WICHARD, 1996, male in lateral view, holotype; GPIMH: 3751.

bifurcation of M in M_{1+2} and M_{3+4}. Cubitus Cu1 divides distally in Cu1a and Cu1b, fork V present. Cubitus Cu2 ends in Cu1b, but slightly touches the wing margin, where a short crossvein to the wing margin is placed. In hindwing (Fig. 30b) a small fork I, fork III, and fork V present, discoidal cell open. Length of forewing: 3.8 mm, of hindwing: 2.5 mm.

Male genitalia represented in Figs. 30c–d and described in JOHANSON & WICHARD (1996).

Helicopsyche (Feropsyche) voigti JOHANSON & WICHARD, 1996

Figs. 31a–c, 32

Holotype: Male embedded in Dominican amber; SMNS: Do-5699 (ex Coll. WICHARD).

Diagnosis. – In forewing (Fig. 31b) fork I ($R_2 + R_3$) and fork II ($R_4 + R_5$) present; bifurcation of R_{2+3} in $R_2 + R_3$ originates laterally on the discoidal cell; discoidal cell closed; bifurcation of R_{4+5} in $R_4 + R_5$ originates at distal crossvein of the discoidal cell. Media M divided in M_{1+2} and in M_{3+4}; fork III ($M_1 + M_2$) present, M_{3+4} present (= fork IV absent); crossvein R_5-M_{1+2} very small, crossvein M-Cu1 at bifurcation of M in M_{1+2} and M_{3+4}; thyridium cell probably closed, longer than discoidal cell. Cubitus Cu1 divides distally in Cu1a and Cu1b, fork V present. Cubitus Cu2 ends in Cu1b, but nearly touches the wing margin, where a very short crossvein to the wing margin is placed. In hindwing fork I ($R_2 + R_3$) is present, discoidal cell open. Fork III ($M_1 + M_2$) seems to be present or possibly M is divided into M_{1+2} and

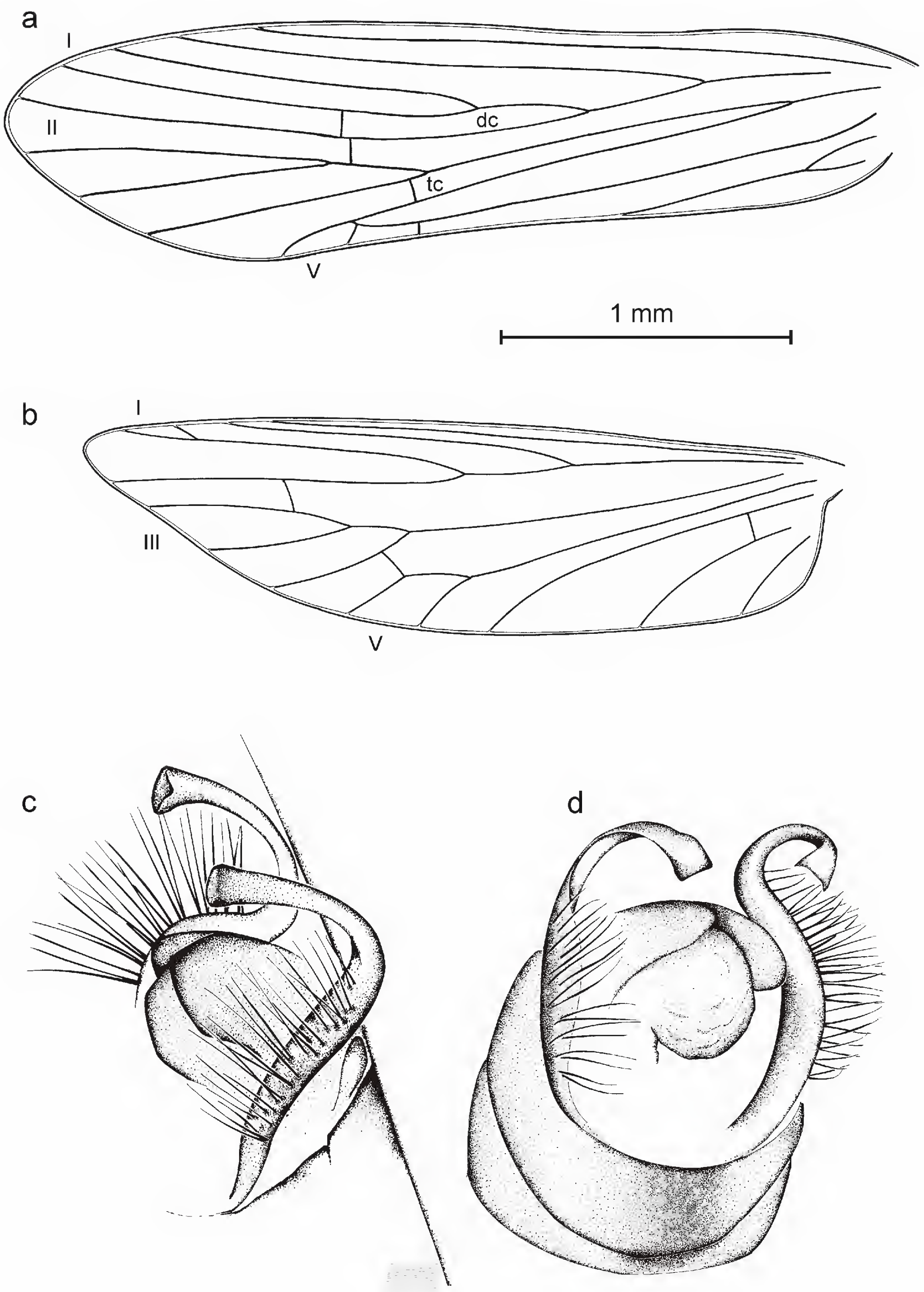

Fig. 30. *Helicopsyche (Feropsyche) electra* Johanson & Wichard, 1996, male, holotype; SMNS: Do-5698 (ex Coll. Wichard); **a**: forewing; **b**: hindwing; **c**: genitalia in lateral view; **d**: genitalia in ventral view.

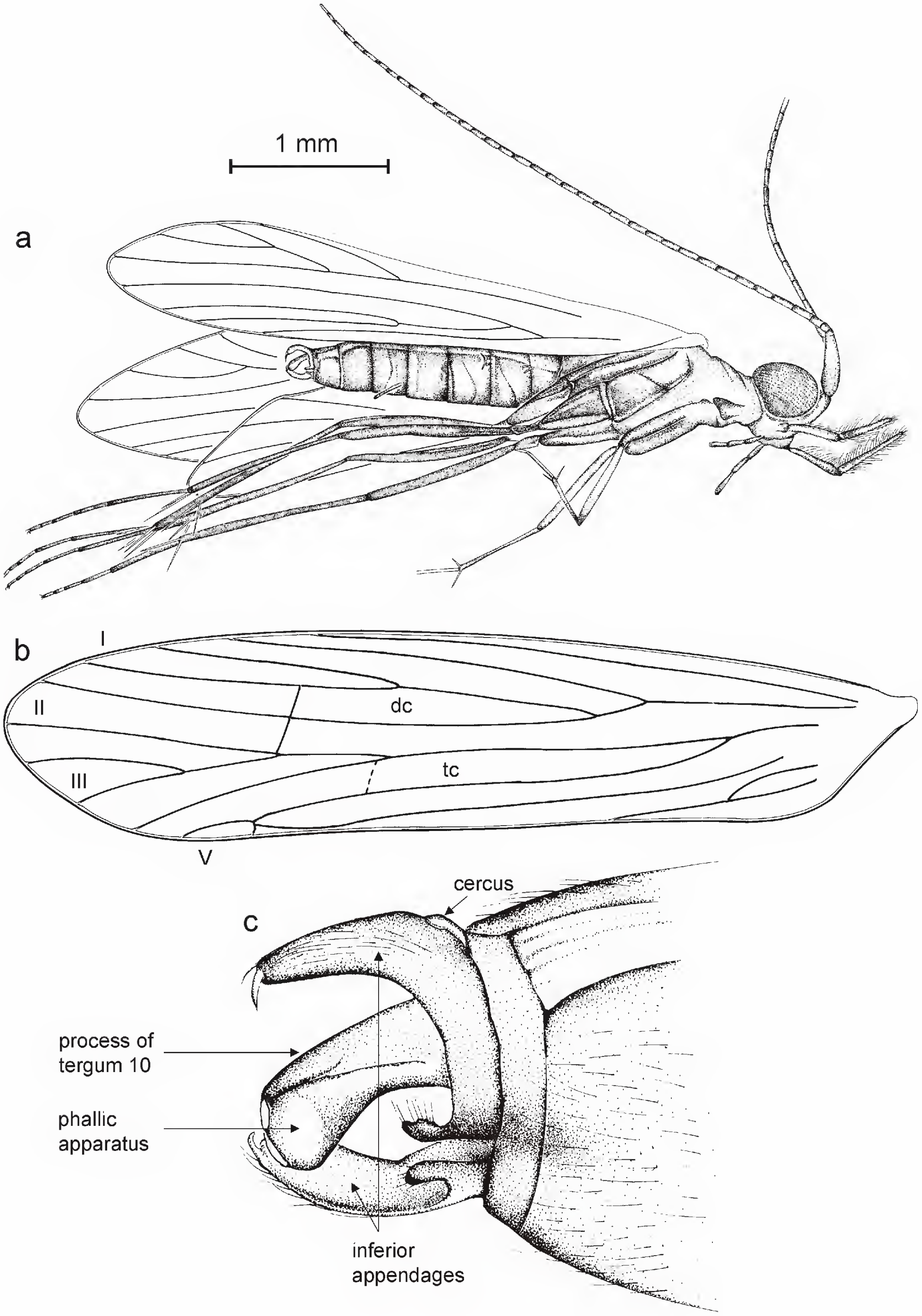
1 mm
a
b
I
II
III
V
dc
tc
c
cercus
process of tergum 10
phallic apparatus
inferior appendages

Fig. 31. *Helicopsyche (Feropsyche) voigti* JOHANSON & WICHARD, 1996, male, holotype; SMNS: Do-5699 (ex Coll. WICHARD); **a**: ventrolateral view; **b**: forewing; **c**: genitalia in ventrolateral view.

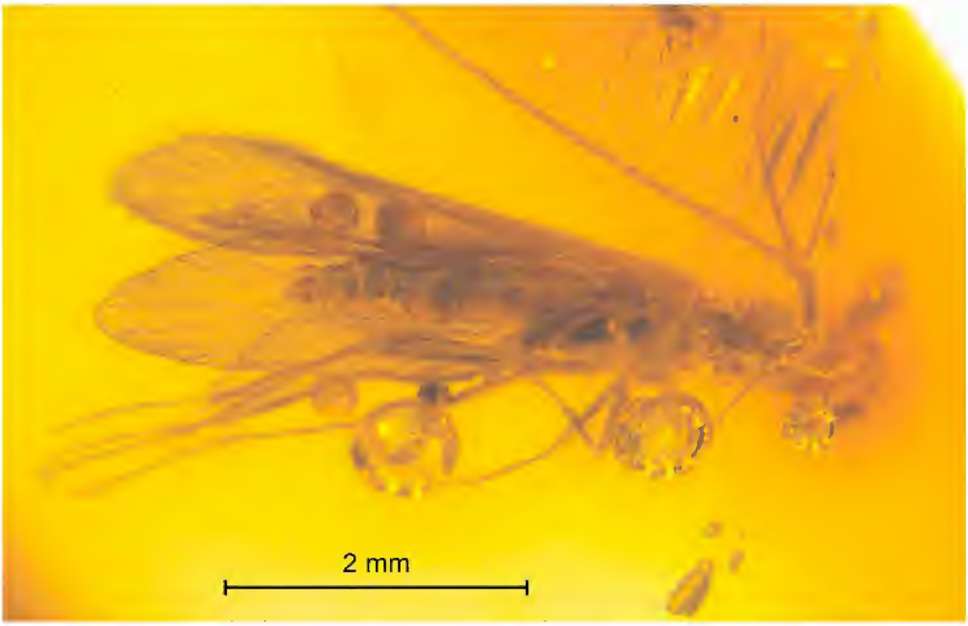

Fig. 32. *Helicopsyche (Feropsyche) voigti* Johanson & Wichard, 1996, male in ventrolateral view, holotype; SMNS: Do-5699 (ex Coll. Wichard).

M_{3+4} at crossvein R_5-M_{1+2}. The hindwing is partly covered by the forewing. Forewing length: 3.7 mm.

Male genitalia represented in Fig. 31c and described in Johanson & Wichard (1996).

4. Discussion

4.1. Aquatic habitats reconstructions

Among all insects of Dominican amber, the included caddisflies are very rarely found representing only 0.1% of all inclusions (Wichard 1987). This low occurrence of caddisflies also seems to characterize Mexican amber (Wichard et al. 2006), whereas in Baltic amber caddisflies are abundantly represented with about 2% (Wichard & Weitschat 1996, 2004). The share of aquatic insects exceeds 25% of all inclusions in Baltic amber (Wichard 2005) with Chironomidae and Trichoptera being the two largest taxonomic groups.

In Dominican amber all other aquatic insects are also scarcely available (Arillo & Ortuno 2005). Of Plecoptera, which are preferably used for the evidence of flowing waters, only one specimen was found so far, being described as fossil species (Perlidae: *Dominoperla antigua* Stark & Lentz, 1992). The Chironomidae (Grund 2005, 2006), the Ephemeroptera (Staniczek 2003), and even the Odonata (Bechly 1993, 2000) appear together in few specimens more frequently than the single Ple-

Tab. 1: Checklist of the extant Hispaniolan Trichoptera (Flint & Sykora 2004) and fossil Trichoptera of Dominican amber (F: undescribed female, L: undescribed larvae).

Family	Genus	Extant species	Fossil species
Suborder Spicipalpia			
Hydrobiosidae	*Atopsyche*	9 (+ 2 F)	1
Glossosomatidae	*Campsiophora*	1	
	Cariboptila	6	
	Cubanoptila		4
Hydroptilidae	*Alisotrichia*	10	1
	Hydroptila	3	
	Leucotrichia	2	1
	Metrichia	5 (+ 1 F)	
	Neotrichia	3 (+ 1 F)	
	Ochrotrichia	10 (+ 2 F)	6
	Oxyethira	10 (+ 1 F)	
Suborder Annulipalpia			
Philopotamidae	*Chimarra (Curgia)*	2	
	Chimarra (Chimarrita)	1	6
	Chimarra (Otarrha)	4	
Hydropsychidae	*Calosopsyche*	4	1
	Macronema	(1 L)	1
	Palaehydropsyche		1
	Streptopsyche	5	
	Smicridea	5 (+ 1 F)	
Ecnomidae	*Austrotinodes*	1	(1 F)
Xiphocentronidae	*Xiphocentron*	2	
Dipseudopsidae	*Antillopsyche*	1	3
Polycentropodidae	*Cernotina*	1	1
	Polycentropus	5	
Suborder Integripalpia			
Calamoceratidae	*Phylloicus*	2	1
Leptoceridae	*Nectopsyche*	1	
	Oecetis	2	
	Setodes	1	2
Odontoceridae	*Marilia*	3	
Helicopsychidae	*Helicopsyche (Feropsyche)*	10	3

coptera. Nevertheless, they represent the rare group of aquatic insects. Based on the detection of these relatively few aquatic insects, it is impossible to describe in detail the inhabited aquatic biota and to visualize running or still water.

Tab. 1 compares the spread of caddisflies on Hispaniola with the fossil records of Dominican amber. 11 of altogether 13 trichopteran families, which are presently identified on the Caribbean isles (Flint & Sykora 2004), do also occur in Dominican amber. The two lacking families are Odontoceridae and Xiphocentronidae. 28 extant genera or rather subgenera are compared with 15 genera of Dominican amber, among which one fossil genus *(Palaehydropsyche)* is extinct and the remaining 14 genera are still existing until today.

The following indications caddisflies provide with 33 fossil species of 14 extant genera that are distributed into 11 families:

Hydrobiosidae, *Atopsyche*: In the Neotropical region, larvae of *Atopsyche* live as predators in slowly and fast running waters, streams, and rivers, few live even in hygropetric habitats (Flint 1963). They are free-living and do not construct a retreat or case until just before pupation, when a closed cocoon is covered by small stones attached to rocks.

Glossosomatidae, *Cubanoptila*: Neotropical larvae of glossosomatids tolerate warm and slowly flowing water (FLINT 1963). They often live in small aggregations on rocks and hand-sized or smaller stones on the ground. The larvae are scrapers and feed on epiphytes and detritus of the stones' surfaces. The larvae of *Cubanoptila* build tortoise-cases (BOTOSANEANU & SYKORA 1973), which are typical of most glossosomatid larvae.

Hydroptilidae, *Alisotrichia, Leucotrichia,* and *Ochrotrichia*: The larvae of all three hydroptilid genera prefer flowing water. Probably they scrape epiphyton from rock- and stone-surfaces. *Ochrotichia* is very common and widely distributed in North-, Central-, and South-America as well as in Dominican amber.

Philopotamidae, *Chimarra*: The genus is species-rich, world-wide distributed, and very common in the Neotropical region (BLAHNIK 1998). The larvae live in flowing water of all types, from large rivers to small streams. They build long, tubular nets and filter fine organic particles from the passing water.

Hydropsychidae, †*Palaehydropsyche, Calosopsyche, Macronema*: The extant genera, *Calosopsyche* and *Macronema*, are rheophilic as all the net-spinning Hydropsychidae.

Ecnomidae, *Austrotinodes*: The larvae of the Neotropical genus *Austrotinodes* seem to prefer large flowing rivers as well as small streams, where they live on the underside of rocks (FLINT 1973). They construct flimsy tubes which are fixed on the rocks with silk. In general ecnomid larvae live in small streams and along the shorelines of lakes.

Dipseudopsidae, *Antillopsyche*: Little is known about the larvae of *Antillopsyche*. FLINT (1964) found larvae in a small, clear stream.

Polycentropodidae, *Cernotina*: Predacious larvae of *Cernotina* are common in lentic or slowly flowing lotic water.

Calamoceratidae, *Phylloicus*: Larvae of *Phylloicus* live in slowly flowing waters and in pools. One species (*Phylloicus bromeliarum* MÜLLER, 1880) inhabits epiphytic bromeliads, called phytotelmata (MÜLLER 1880). *Phylloicus* larvae construct flattened cases using leafs cut into ovals and are feeding as shredders on the same leaf litter they are using to construct their cases (FLINT et al. 1999, PRATHER 2003).

Leptoceridae, *Setodes*: This genus is unknown in Middle and South America except in Dominican amber (FLINT et al. 1999, WICHARD 1995b). In North America the larvae live in cool, running waters and also along the shores of lakes. The biology of larvae and pupae is described by MERRILL & WIGGINS (1971).

Helicopsychidae, *Helicopsyche (Feropsyche)*: *Helicopsyche* of Neotropics belong to the subgenus *Feropsyche* (JOHANSON, 1998). The larvae build helical caves of sand grains. They are scrapers and feed on epiphyts of the rocks. The larvae occur in streams and rivers as well as in springs and along lake shores.

The short characterization of Neotropical genera, which occur also in Dominican amber, is based on extant species and indicates that probably all genera of Dominican amber caddisflies prefer flowing waters. Not a single genus is exclusively dependant on lentic waters. Three of fifteen genera only occur in lotic as well as in lentic waters.

This ecologic characterization very possibly asserts that about 15–20 million years ago nearly exclusively flowing water ecosystems dominated Hispaniola. According to the bordered size of Hispaniola there probably existed no large running waters, but rather small rivers and streams, which flowed with a moderate decline from upland to valley.

Flowing waters are not only essential for the rheophilous larvae of caddisflies but also for the genesis of amber. The resin-producer is the deciduous tree of the genus *Hymenaea* (Leguminosae), which belonged to the tree-population of the humid tropical mountain forest of the Miocene 15–20 million years ago (Poinar & Poinar 1999). For the genesis of amber flowing waters were necessary routes of transportation, carrying the resin from the mountain forest to the coasts of the Caribbean Sea. Along the seashore the resin was embedded in marine sand and generated into solid amber through chemo-physical processes over thousands or millions of years.

A comparison with the genesis of the Baltic amber reveals that wide differences do not only consist in the age (40–50 million years ago of the Eocene Baltic amber and 16–20 million years ago of the Miocene Dominican amber). In the course of several millions of years and from a much larger area, the water-carriage of broad rivers and flood-plains transported a huge amount of resin from the Baltic amber forests to the sea. In contrast, flowing waters and their drifted amount of resin from the mountain forests of the Cordilleras of the comparatively small isle of Hispaniola are inevitably very restricted.

The inclusions of aquatic insects indicate that on Hispaniola at Miocene most flowing waters were probably small and occurred with a much lower frequency in the mountain forest than comparatively in the Baltic amber forest at the Eocene period. The flowing waters were not sufficient in number and in size to transport a great amount of resin which is found as amber today. Climatic events with heavy precipitations might have flooded the land and additionally drifted the majority of tree-resin out of the deadwood into the sea. The participation of flowing waters in the genesis of amber was evidently not very significant.

4.2. Biogeographical aspects

On 2nd International Symposium on Trichoptera Flint (1978) reported that over 80% of all Trichoptera in the Antilles are single-island endemics. The trichopteran fauna of the Greater Antilles is quite different from that of the Lesser Antilles. It seems that the Greater Antilles and Lesser Antilles were colonized separately, at a different time and from different places. The fauna of the Lesser Antilles is related to the caddisflies of northern South America. The trichopteran fauna of Greater Antilles seems to have been isolated for a long time and combines three elements of relationships: 1. the North American lineage, 2. the South American lineage, and 3. the African lineage.

Compared with the dominant transcontinental invasion on the "North American-Caribbean track" and on the "South American-Caribbean track" (Rosen 1975) the invasion from Africa is of small importance. Nevertheless, the African lineage dominates the trichopteran fauna of the Miocene Dominican amber. More than 50% of all Trichoptera found in Dominican amber belong to genus *Antillopsyche*, which is spread to the three fossil species *A. oliveri*, *A. auricula*, and *A. digitus*. *Antillopsyche* is closely related to *Pseudoneureclipsis* together forming the subfamily Pseudoneureclipsinae. The subfamily is distributed from Ethiopian and Oriental regions to the Greater Antilles when South America jointed to Africa at Mesozoic period. Another fossil species, *Antillopsyche mexicana* from the Miocene, is also verified in Mexican amber (Wichard et al. 2006). The amber fossils demonstrate that genus *Antillopsyche* was common in Miocene of the Greater Antilles and distributed probably from Caribbean to Central America. Today four extant species of *Antillopsyche* are endemic on the islands of the Greater Antilles: Cuba *(A. aycara, A. wrighti)*, Hispaniola *(A. demma)*, and Puerto Rico *(A. tubicola)* (Flint et al. 1999). Four fossil species from Miocene correspond with four extant species. And the extant *Antillopsyche demma* seems to be closely related to fossil *A. mexicana* and *A. auricula*.

Another biogeographical aspect demonstrates *Cubanoptila* of the family Glossosomatidae. With five extant species, the genus *Cubanoptila* occurs exclusively on the island of Cuba. It is remarkable that the endemic genus is also represented by four species in the Miocene Dominican amber on the neighbouring island Hispaniola, whereas extant species of *Cubanoptila* are missing on Hispaniola, so far (Tab. 1). The majority of the species in the Caribbean consist of single-island endemics (Flint 1978), although some other endemic species are distributed on the larger islands, such as Cuba and Hispaniola.

Endemic genera or genera with pan-Caribbean distribution which occur in the Miocene Dominican amber inclusions and in the present (genus *Antillopsyche*, genus *Cubanoptila*), point out a high continuity of their habitats. Through an amphibious life circle with terrestrial imagines and aquatic larvae and pupae, the survival is advantaged even if dramatic climate changes interfere with the terrestrial stage. In aquatic habitats extern climate interferences can be compensated.

Freshwater ecosystems produce more ecological stability than terrestrial ecosystems, when atmospheric and global changes challenge freshwater and terrestrial ecosystems.

5. Overview of order Trichoptera in Dominican amber

The classification below is structured to the world fauna by Frannia & Wiggins (1997) and presents the family-, genus- and species-taxa, verified in Dominican amber and their holotypes. The preliminary list (Wichard 1987) of caddisflies in Dominican amber is outdated.

Suborder Spicipalpia (Cocoon-Making Caddisflies)

Family Hydrobiosidae

Atopsyche perlucida n. sp.	SMNS: Do-5711

Family Glossosomatidae

Cubanoptila grimaldii Wichard, 1995	AMNH: DR-10-72
Cubanoptila mederi Wichard, 1989	NMNH
Cubanoptila poinari Wichard, 1989	OSUC: TR-2-4
Cubanoptila longiscapa n. sp.	SMNS: Do-5712

Family Hydroptilidae

Alisotrichia arizela Wells & Wichard, 1989	SMNS: Do-5700
Leucotrichia adela Wells & Wichard, 1989	NMNH
Ochrotrichia aldama (Mosely, 1937)	SMNS: Do-5702
Ochrotrichia aliceae Wichard, 2000	NMNH: ENT-I-17891
Ochrotrichia brodzinskyi Wells & Wichard, 1989	SMNS: Do-5701
Ochrotrichia chaulioda Wells & Wichard, 1989	NMNH
Ochrotrichia denaia Wells & Wichard, 1989	NMNH
Ochrotrichia doehleri Wichard, 1981	SMNS: Do-5703

Suborder Annulipalpia (Retreat-Making Caddisflies)

Family Philopotamidae

Chimarra (Chimarrita) dommeli Wichard, 1983	SMNS: Do-5707
Chimarra (Chimarrita) succini Wichard, 1983	SMNS: Do-3386-M-1
Chimarra (Chimarrita) palaedominicana Wichard, 1983	SMNS: Do-5706
Chimarra (Chimarrita) resinae Wichard, 1983	SMNS: Do-5705
Chimarra (Chimarrita) weitschati Wichard, 1983	GPIMH: 2534
Chimarra (Chimarrita) palaenova n. sp.	SMNS: Do-5713

Family Hydropsychidae

Palaehydropsyche fossilis Wichard, 1986	BMNH: 64598
Calosopsyche palaeoelegans n. sp	SMNS: Do-820-K
Macronema hispaniola n. sp.	SMNS: Do-2219-K

Family Ecnomidae

Austrotinodes sp. (innominate female)	SMNS: Do-4143-M

Family Dipseudopsidae

Antillopsyche auricula n. sp.	SMNS: Do-5714
Antillopsyche digitus n. sp.	SMNS: Do-5715
Antillopsyche oliveri Wichard, 1985	SMNS: Do-5708

Family Polycentropodidae

Cernotina pulchra n. sp.	SMNS: Do-5716

Suborder Integripalpia (Case-Making Caddisflies)

Family Calamoceratidae

Phylloicus velteni n. sp.	SMNS: Do-5717

Family Leptoceridae

Setodes resinacapta Wichard, 1995	NMNH: ENT-I-7049
Setodes aureoinclusa Wichard, 1995	NMNH: ENT-I-10680

Family Helicopsychidae

Helicopsyche (Feropsyche) scaloida Johanson & Wichard, 1996	GPIMH: 3751
Helicopsyche (Feropsyche) electra Johanson & Wichard, 1996	SMNS: Do-5698
Helicopsyche (Feropsyche) voigti Johanson & Wichard, 1996	SMNS: Do-5699

6. References

Arillo, A. & Ortuno, V. M. (2005): Catalogue of fossil insect species described from Dominican amber (Miocene). – Stuttgarter Beiträge zur Naturkunde, Serie B, **352**: 68 pp.

Bechly, G. (1993): Fossil odonates in Dominican and Baltic amber. – Argia, **5**: 13–15.

Bechly, G. (2000): A new fossil damselfly species (Insecta: Odonata: Zygoptera: Coenagrionidae: Ischnurinae) from Dominican Amber. – Stuttgarter Beiträge zur Naturkunde, Serie B, **299**: 9 pp.

Blahnik, R. J. (1997): Systematics of *Chimarrita*, a new subgenus of *Chimarra* (Trichoptera: Philopotamidae). – Systematic Entomology, **22**: 199–243.

Blahnik, R. J. (1998): A revision of the Neotropical species of the genus *Chimarra*, subgenus *Chimarra* (Trichoptera: Philopotamidae). – Memoirs of the American Entomological Institute, **59**: 1–318.

Botosaneanu, L. (1990): Results of a trichopterological (Insecta: Trichoptera) travel to the Lesser Antilles in 1989. – Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie, **60**: 39–48.

Botosaneanu, L. & Sykora, J. (1973): Sur quelques Trichoptères (Insecta: Trichoptera) de Cuba. – Résultats des Expéditions Biospéologiques cubano-roumaines à Cuba, **1**: 379–407; Bucharest.

Flint, O. S. (1963): Studies of Neotropical caddis flies, I: Rhyacophilidae and Glossosomatidae (Trichoptera). – Proceedings of the United States National Museum, **114**: 453–478.

Flint, O. S. (1964): The caddisflies (Trichoptera) of Puerto Rico. – University of Puerto Rico, Agricultural Experiment Station, Technical Paper, **40**: 1–80.

Flint, O. S. (1973): Studies of Neotropical caddis flies, XVI: The genus *Austrotinodes* (Trichoptera: Psychomyiidae). – Proceedings of the Biological Society of Washington, **86**: 127–142.

Flint, O. S. (1978): Probable origins of the West Indian Trichoptera and Odonata faunas. – In: Crichton, M. I. (ed.): Proceedings of the 2nd International Symposium on Trichoptera 1977: 215–228; The Hague (Junk).

Flint, O. S. & Bueno Soria, J. (1979): Studies of Neotropical caddisflies, XXIV. The genus *Macronema* in Mesoamerica (Trichoptera: Hydropsychidae). – Proceedings of the Entomological Society of Washington, **81**: 522–535.

Flint, O. S. & Bueno Soria, J. (1982): Studies of Neotropical caddisflies, XXXII. The immature stages of *Macronema variipenne* Flint & Bueno, with the division of *Macronema* by the resurrection of *Macrostemum* (Trichoptera: Hydropsychidae). – Proceedings of the Biological Society of Washington, **95**: 358–370.

Flint, O. S. & Bueno Soria, J. (1987): Studies of Neotropical caddisflies, XXXVI. The genus *Calosopsyche* in Central America, with descriptions of its immature stages (Trichoptera: Hydropsychidae). – In: Bournaud, M. & Tachet, H. (eds.): Proceedings of the Fifth International Symposium on Trichoptera, 29–37; The Hague (Junk).

Flint, O. S., Holzenthal, R. W. & Harris, S. C. (1999): Catalog of the Neotropical Caddisflies (Insecta: Trichoptera). 239 pp; Columbus (Ohio Biological Survey).

Flint, O. S. & Sykora, J. (2004): Caddisflies of Hispaniola, with special reference to the Dominican Republic (Insecta: Trichoptera). – Annals of Carnegie Museum, **73**: 1–60.

Frania, H. E. & Wiggins, G. B. (1997): Analysis of morphological and behavioural evidence for the phylogeny and higher classification of Trichoptera (Insecta). – Royal Ontario Museum, Life Sciences Contributions, **160**: 1–68.

GRUND, M. (2005): Chironomids (Diptera: Chironomidae) of Dominican amber. *Ablabesmyia electrohispaniolana*, sp. n. and paleoecological indications due to subfamily proportions. – Insect Systematic Evolution, **36**: 29–34.

GRUND, M. (2006): Chironomidae (Diptera) in Dominican amber as indicators for ecosystem stability in the Caribbean. – Palaeogeography, Palaeoclimatology, Palaeoecology, **241**: 410–416.

HENWOOD, A. A. (1993): Ecology and taphonomy of Dominican Republic amber and its inclusions. – Lethaia, **26**: 237–245.

HOLZENTHAL, R. W. & CRESSA, C. (2002): The Trichoptera, Caddisflies, of Venezuela: Three new species and records of *Atopsyche* BANKS (Hydrobiosidae). – Studies on Neotropical Fauna and Environment, **37**: 133–143.

ITURRALDE-VINENT, M. A. (2001): Geology of the amber-bearing deposits of the Greater Antilles. – Caribbean Journal of Science, **37**: 141–167.

ITURRALDE-VINENT, M. A. & MACPHEE, R. D. E. (1996): Age and paleogeographical origin of Dominican Amber. – Science, **273**: 1850–1852.

JOHANSON, K. A. (1995): A catalog of the Helicopsychidae (Insecta: Trichoptera) of the World. – Bulletin Zoölogisch Museum, Universiteit van Amsterdam, **14**: 101–124.

JOHANSON, K. A. (1998): Phylogenetic and biogeographic analysis of the family Helicopsychidae (Insecta: Trichoptera). – Entomologica Scandinavica, Supplement **53**: 1–172.

JOHANSON, K. A. & WICHARD, W. (1996): Caddis flies of Dominican Amber – X. Fossil species of Helicopsychidae (Trichoptera). – Mitteilungen aus dem Geologisch-Paläontologischen Institut und Museum der Universität Hamburg, **79**: 195–209.

MERRILL, D. & WIGGINS, G. B. (1971): The larva and pupa of the caddisfly genus *Setodes* in North America (Trichoptera: Leptoceridae). – Royal Ontario Museum, Life Sciences, Occasional Papers, **19**: 1–12.

MÜLLER, F. (1880): Über die von den Trichopterenlarven der Provinz Santa Catharina verfertigten Gehäuse. – Zeitschrift für Wissenschaftliche Zoologie, **35**: 47–87.

POINAR, G. & POINAR, R. (1994): The Question for Life in Amber. 219 pp.; New York (Addison-Wesley Publishing Company).

POINAR, G. & POINAR, R. (1999): The amber forest. A reconstruction of a vanished world. 239 pp.; Princeton (Princeton University Press).

PRATHER, A. L. (2003): Revision of the Neotropical caddisfly genus *Phylloicus* (Trichoptera: Calamoceratidae). – Zootaxa, **275**: 1–214.

ROSEN, D. E. (1975): A vicariance model of Caribbean biogeography. – Systematic Zoology, **24**: 431–464.

ROSS, H. H. & KING, E. W. (1952): Biogeographic and taxonomic studies in *Atopsyche* (Trichoptera, Rhyacophilidae). – Annals of the Entomological Society of America, **45**: 177–204.

ROSS, H. H. & UNZICKER, J. D. (1977): The relationships of the genera of American Hydropsychinae as indicated by phallic structures (Trichoptera, Hydropsychidae). – Journal of the Georgia Entomological Society, **12**: 298–312.

SCHMID, F. (1989): Les Hydrobiosides (Trichoptera, Annulipalpia). – Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie, **59** (supplement): 1–154.

STANICZEK, A. H. (2003): New fossil mayflies from Dominican amber (Insecta: Ephemeroptera: Leptophlebiidae: Atalophlebiinae). – Stuttgarter Beiträge zur Naturkunde, Serie B, **341**: 22 pp.

WELLS, A. & WICHARD, W. (1989): Caddisflies of Dominican Amber. VI. Hydroptilidae (Trichoptera). – Studies on Neotropical Fauna and Environment, **24**: 41–51.

WICHARD, W. (1981): Köcherfliegen des Dominikanischen Bernsteins. – I. *Ochrotrichia doehleri* sp. nov. (Trichoptera, Hydroptilidae). – Mitteilungen der Münchner Entomologischen Gesellschaft, **71**: 161–162.

WICHARD, W. (1983a): Köcherfliegen des Dominikanischen Bernsteins. – II. Fossile Arten der Gattung *Chimarra* (Trichoptera, Philopotamidae). – Mitteilungen der Münchner Entomologischen Gesellschaft, **72**: 137–145.

WICHARD, W. (1983b): Köcherfliegen des Dominikanischen Bernsteins. – III. *Chimarra succini* n. sp. (Stuttgarter Bernsteinsammlung: Trichoptera, Philopotamidae). – Stuttgarter Beiträge zur Naturkunde, Serie B, **95**: 8 pp.

Wichard, W. (1985): Köcherfliegen des Dominikanischen Bernsteins. – IV. *Antillopsyche oliveri* spec. nov. (Trichoptera, Polycentropodidae). – Studies on Neotropical Fauna and Environment, **20**: 117–124.

Wichard, W. (1986): Köcherfliegen des Dominikanischen Bernsteins. – V. *Palaehydropsyche fossilis* gen. n. sp. n. (Trichoptera, Hydropsychidae). – Studies on Neotropical Fauna and Environment, **21**: 189–195.

Wichard, W. (1987): Caribbean amber caddisflies – Biogeographical aspects. – In: Bourneaud, M. & Tachet, H. (eds.): Proceedings of 5th International Symposium on Trichoptera, Lyon 1986: 67–69; The Hague (Jung).

Wichard, W. (1989): Köcherfliegen des Dominikanischen Bernsteins. VII. Fossile Arten der Gattung *Cubanoptila* (Trichoptera, Glossosomatidae). – Mitteilungen der Münchner Entomologischen Gesellschaft, **79**: 91–100.

Wichard, W. (1995a): Köcherfliegen des Dominikanischen Bernsteins. – VIII. *Cubanoptila grimaldii* n. sp., eine weitere fossile Art der Glossosomatidae (Insecta, Trichoptera). – Mitteilungen aus dem Geologisch-Paläontologischen Institut und Museum der Universität Hamburg, **78**: 159–165.

Wichard, W. (1995b): Köcherfliegen des Dominikanischen Bernsteins. – IX. Fossile Leptoceridae der Gattung *Setodes* Rambur, 1842 (Insecta, Trichoptera). – Mitteilungen aus dem Geologisch-Paläontologischen Institut und Museum der Universität Hamburg, **78**: 167–177.

Wichard, W. (2000): Köcherfliegen des Dominikanischen Bernsteins. XI. *Ochrotrichia aliceae* n. sp., eine neue fossile Hydroptilidae. – Mitteilungen aus dem Geologisch-Paläontologischen Institut und Museum der Universität Hamburg, **84**: 241–246.

Wichard, W. (2005): Wasserinsekten im Baltischen Bernstein. – Biologie in unserer Zeit, **35**: 83–89.

Wichard, W. & Weitschat, W. (1996): Wasserinsekten im Bernstein – eine paläobiologische Studie. – Entomologische Mitteilungen aus dem Löbbecke-Museum + Aquazoo, Düsseldorf, Beiheft **4**: 1–122.

Wichard, W. & Weitschat, W. (2004): Im Bernsteinwald. 168 pp.; Hildesheim (Gerstenberg).

Wichard, W., Solorzano Kraemer, M. M. & Luer, C. (2006): First caddisfly species from Mexican amber (Insecta: Trichoptera). – Zootaxa, **1378**: 37–48.

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Laubmoose (Bryophyta, Bryopsida) aus dem Miozän der Oberlausitz (Sachsen, Deutschland)

Mosses (Bryophyta, Bryopsida) from the Miocene of the Upper Lusatia (Saxony, Germany)

JAN-PETER FRAHM, MARKUS PREUSSING & HENRIETTE JECHOREK

Abstract

This study presents six moss species from allochthonous taphocoenoses of limnic-fluviatile sediments of two sites in the Upper Lusatia (Saxony, Germany) with plant macro remains from the Middle Miocene (approx. 16–11 m.a.). Two of these species belong to the genus *Rhizogonium* and are not identical with currently known species. They are newly described as *R. hattorioides* n. sp. and *R. antiquum* n. sp. Two pleurocarpous mosses are newly described as *Isopterygiites proratus* n. gen. n. sp. and *Meteorium antiquum* n. sp. Further, the two recent moss species *Homalia lusitanica* and *Andoa* cf. *berthelotiana* were detected which are known from the Miocene, respectively Pliocene. The detection of the two new *Rhizogonium* species is particularly noteworthy, since this genus does not belong to the recent European flora and only two fossils from a con-generic species exist from here. In total, the detected moss species are temperate, mediterranean and tropical montane elements, corresponding to the phanerogamic flora which forms forests with different proportions of deciduous and evergreen trees and shrubs.

Keywords: Fossil mosses, Bryopsida, *Rhizogonium hattorioides* n. sp, *Rhizogonium antiquum* n. sp., *Isopterygiites proratus* n. gen. n. sp., *Meteorium antiquum* n. sp., Miocene, Upper Lusatia, Palaeobotany.

Zusammenfassung

Von zwei Fundstellen pflanzlicher Makroreste aus dem Mittelmiozän (ca. 16–11 Ma) der Oberlausitz (Sachsen, Deutschland) werden sechs Moosfunde aus allochthonen Taphozönosen limnisch-fluviatiler Sedimentablagerungen vorgestellt. Die beiden akrokarpen Laubmoose *Rhizogonium hattorioides* n. sp. und *Rhizogonium antiquum* n. sp. sowie die zwei pleurokarpen Arten *Isopterygiites proratus* n. gen. n. sp. und *Meteorium antiquum* n. sp. werden neu beschrieben. Ferner können die beiden rezenten Arten *Homalia lusitanica* und *Andoa* cf. *berthelotiana* nachgewiesen werden, welche bereits aus dem Mio- bzw. Pliozän bekannt sind. Hervorzuheben ist der Nachweis der neuen *Rhizogonium*-Arten, da die Gattung rezent in Europa nicht vorkommt und bisher fossil hier nur ein anderer Vertreter dieser Gattung mit zwei Funden bekannt war. Die beschriebenen Moosarten stellen temperate, mediterrane und tropisch-montane Florenelemente dar, die sich gut in das anhand der Phanerogamen-Flora re-

konstruierte Vegetationsbild von Wäldern, die sich aus sommer- und immergrünen Gehölzen zusammensetzen, einfügen.

1. Einleitung

Fossile Nachweise von Moosen sind vor allem aufgrund ihres zarten Baues (u.a. durch das Fehlen von Lignin) selten. Aus dem Devon sind lediglich 4, dem Karbon 14, dem Perm 35, der Trias 20, dem Jura 26 und der Kreide 25 Moosarten nachgewiesen (FRAHM 2001b). Im Tertiär sind insgesamt ca. 180 Laubmoosarten (ohne Berücksichtigung von Formgattungen) bekannt. Dabei sind quantitative Angaben aufgrund der Unsicherheit der taxonomischen Zuordnung der Proben nur näherungsweise möglich. Aus dem Tertiär Europas sind etwa 150 Arten nachgewiesen, von denen 23 ausgestorben sind (FRAHM 2000). Der größte Teil der Nachweise stammt mit 95 Arten aus dem Pliozän (FRAHM 2000). Den zweitgrößten Anteil stellen Bernsteininklusen aus dem Eozän mit mehr als 50 Arten (FRAHM 2001a, FRAHM 2004). Aus dem Paleozän sind keine, aus dem Oligozän 4 und aus dem Miozän 49 Arten bekannt (FRAHM 2004). Von den aus dem Neogen (Mio- und Pliozän) bekannten Arten existieren heute noch 108 (76 aus Europa, 32 weitere aus Nordamerika; MILLER 1984). Nur wenige der fossilen Nachweise aus dem Neogen können heute unbekannten Gattungen oder ausgestorbenen Arten heutiger Gattungen zugeschrieben werden. Das bedeutet, dass die Artenzusammensetzung der Moosflora des Neogens in Europa weitgehend der heutigen gleicht und seitdem nur wenige Arten erloschen sind. Aufgrund der erheblichen Klimaveränderungen und der damit verbundenen Arealverschiebungen unterscheiden sich jedoch die heutigen Regionalfloren von den historischen Regionalfloren grundsätzlich in ihrer jeweiligen Artzusammensetzung. Viele Moosarten waren im Neogen nördlicher und westlicher verbreitet als heute (MILLER 1984). Relikte der neogenen Festlandsflora von Europa sind beispielsweise auf den Makaronesischen Inseln erhalten. Zu ihnen gehören die auch von uns nachgewiesene *Andoa berthelotiana* (fossil in Georgien) und die Gattung *Echinodium* JUR., welche rezent mit mehreren Arten vorkommt und fossil durch *Echinodium savicziae* ABRAMOVA & I. I. ABRAMOV in Georgien sowie Polen vertreten ist.

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2. Material

Die vorliegenden Aufsammlungen von Moosresten stammen zum einen (Präparate mit den Inventarnummern 13232, 13233) aus den tonig-schluffigen Ablagerungen des Zwischenmittels 11 im Braunkohlentagebau Berzdorf (TIETZ & CZAJA 2004),

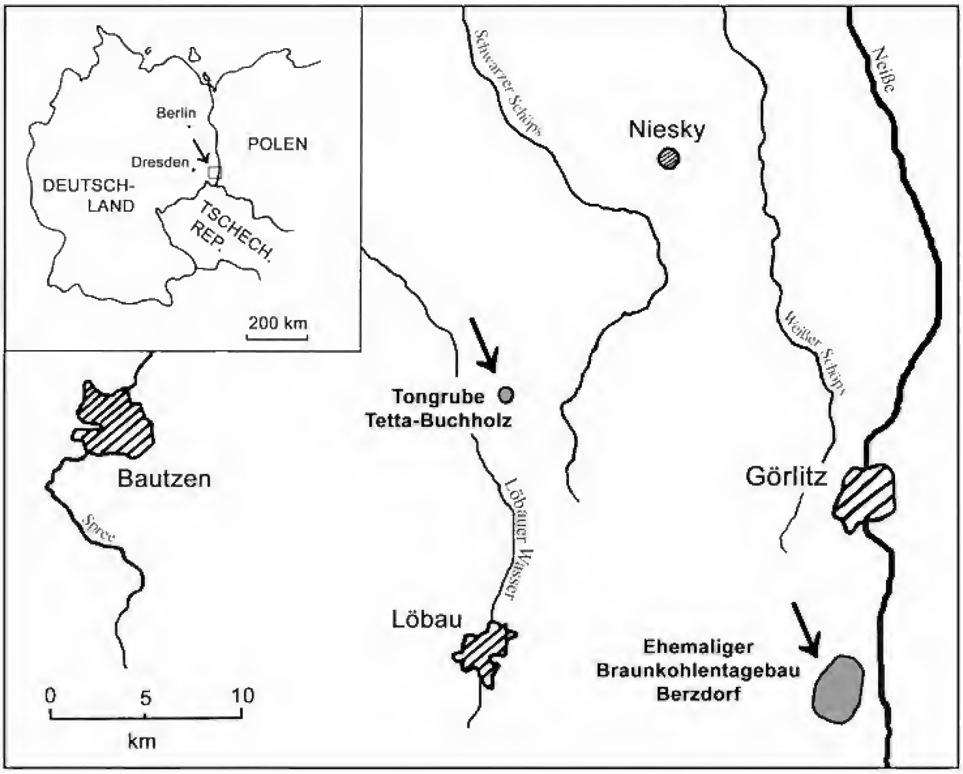
Berlin
POLEN
Dresden
DEUTSCH-
LAND
TSCHECH.
REP.
200 km
Schwarzer Schöps
Niesky
Neiße
Weißer Schöps
Tongrube
Tetta-Buchholz
Bautzen
Spree
Görlitz
Löbauer Wasser
Löbau
Ehemaliger
Braunkohlentagebau
Berzdorf
0
5
10
km

Abb. 1: Geografische Lage der Tongrube Tetta-Buchholz und des ehemaligen Braunkohlentagebaus Berzdorf in der Oberlausitz (Sachsen), nach Czaja & Berner (1999), Skizze stark verändert.

der sich ca. 10 km südlich der Stadt Görlitz befindet (Abb. 1). Mit Hilfe einer sehr artenreichen Frucht- und Samenflora konnte eine biostratigraphische Einstufung der fossilführenden Sedimente in den mittelmiozänen Florenkomplex Kleinleipisch-Františkove Lázně erfolgen (Florenkomplex und biostratigraphische Zuordnung nach Mai 1995, 2001, Czaja 2003, Tietz & Czaja 2004). Zum anderen (Präparate mit den Inventarnummern 13234, 13235, 13236) stammen die Moosreste aus sandigen Sedimentlagen der Tongrube Tetta-Buchholz, die ca. 20 km nordwestlich von Görlitz gelegen ist (Abb. 1). Die hier vorliegende fossile Karpoflora wurde von Czaja & Berner (1999) vorerst dem mittelmiozänen Florenkomplex Klettwitz-Salzhausen biostratigraphisch zugeordnet. Nach Mai (2001: 53) ist eine Einstufung in den nächst älteren Florenkomplex Kleinleipisch-Františkove Lázně sehr wahrscheinlich. Die überlieferten Moose (außer Präparat 13236) wurden in den allochthonen Taphozönosen der Frucht- und Samenfloren vorgefunden. Das Pflanzenmaterial stammt somit ursprünglich aus der weiteren Umgebung und nicht direkt vom ehemaligen Wuchsort. Es unterlag vor der Einbettung im Sediment einem fluviatilen Transport. Das Moosexemplar im Präparat 13236 wurde bei der Aufbereitung fossiler Blätter aus tonig-schluffigem Sediment geborgen und ist parautochthonen oder autochthonen Ursprungs.

Aus dem Artenspektrum der fossilen Frucht- und Samenfloren konnte für die Lokalität Tetta-Buchholz ein Gemischter Mesophytischer Wald (Mixed Mesophytic Forest) und für Berzdorf ein Gemischter Mesophytischer Wald bzw. ein Lorbeer-Sommerwald als zonale Vegetation rekonstruiert werden (CZAJA & BERNER 1999, CZAJA 2003). Die Vegetation beider Fundstellen ist durch das Vorkommen der für das Unter- und Mittelmiozän typischen Jüngeren Mastixioideenfloren (MAI 1964) mit subtropischen immergrünen und zahlreichen gemäßigten sommergrünen Elementen gekennzeichnet. Nach der Zusammensetzung der Makroflora kann für das Mittelmiozän von Berzdorf von einem warmtemperaten bis subtropischen Klima mit einer Temperatur von 14–18 °C im Jahresmittel und einem mittleren Niederschlag über 800 mm/a ausgegangen werden (CZAJA 2003). Die Flora von Tetta-Buchholz spricht für ein warmtemperates, humides und schwach wintertrockenes Klima mit einer mittleren Jahrestemperatur von 13–17 °C und mittleren Niederschlägen von 500–1500 mm (MAI 2001).

Alle Moosreste wurden auf Objektträgern in Glyceringelatine eingebettet und anschließend mit Deckglas und farblosem Nagellack versiegelt. Diese Dauerpräparate befinden sich in der Geowissenschaftlichen Sammlung des Staatlichen Museums für Naturkunde Görlitz (SMNG).

3. Taxonomie

Die Nomenklatur folgt GOFFINET & BUCK (2004).

Abteilung Bryophyta SCHIMP.
Klasse Bryopsida (LIMPR.) ROTHM.
Ordnung Rhizogoniales (M. FLEISCH.) GOFFINET & W. R. BUCK
Familie Rhizogoniaceae BROTH.

Gattung *Rhizogonium* BRID.

Die Gattung *Rhizogonium* ist erst kürzlich revidiert worden (FRAHM et al. 2003). Es werden weltweit sieben rezente Arten akzeptiert. Im vorliegenden fossilen Material sind zwei *Rhizogonium*-Arten zu finden, die keiner der rezenten Arten zugeordnet werden können. Bislang wurde erst ein fossiler Vertreter dieser Gattung, allerdings ohne genaue Artbezeichnung, aus dem Baltischen Bernstein des Eozäns in der Literatur beschrieben (FRAHM 2001a, 2004). Diese Art hat schmal-lanzettliche Blätter und unterscheidet sich dadurch von den hier beschriebenen Arten. Wie häufig bei der Beschreibung von Moosen im Bernstein angeführt wird, sind die fossilen Pflanzen deutlich, in der Regel um die Hälfte, kleiner als die rezenten Vertreter (FRAHM 2004). Dies könnte darauf zurückgeführt werden, dass nur kleinwüchsige Fragmente in den Bernstein eingeweht worden und somit erhalten sind. Aber auch Mooseinschlüsse in situ, wie z.B. auf ganzen Borkenstücken, sind oft auffallend klein. Die beiden vorliegenden Arten sind ebenfalls von erheblich geringerer Größe als die rezenten Vertreter der Gattung. Bemerkenswert ist, dass *R. hattorioides* in allen weiteren Merkmalen mit der rezenten Vergleichsart gut übereinstimmt (s.u.).

Rhizogonium hattorioides J.-P. Frahm & Preussing n. sp.

Taf. 1

Holotypus: SMNG/Geowissenschaftliche Sammlung, Nr. 13236
Derivatio nominis: Im Artnamen soll zum Ausdruck kommen, dass *Rhizogonium hattorii* wahrscheinlich die nächstverwandte Art ist.
Locus typicus: Tongrube Tetta-Buchholz (Sachsen, Oberlausitz).
Stratum typicum: Mittelmiozän, Florenkomplex Kleinleipisch-Františkove Lázně.

Diagnose (lateinisch). – Rhizogonio hattorii valde similis, staturae et cellulis laminalibus minoribus.

Diagnose (deutsch). – Sehr ähnlich *Rhizogonium hattorii*, aber Pflanze und Blattzellen kleiner.

Beschreibung. – Pflanzenfragment 2,4 mm lang, mit 15 Blättern (Taf. 1a). Blätter zweizeilig, nicht herablaufend, breit elliptisch, am Grunde kontrahiert, zwei- bis dreimal so lang wie breit, 0,35–0,66 mm lang und 0,19–0,27 mm breit (Taf. 1a, b, d); Blattrippe zwei Drittel bis drei Viertel der Blattlänge erreichend (Taf. 1b, d); Blattrand ungesäumt, in der oberen Blatthälfte grob ungleichmäßig gezähnt, Zähne einzellig (Taf. 1c, e, f). Laminazellen der Blattspitze relativ dünnwandig, glatt, rhombisch, 10–25 × 8–12 µm groß (Taf. 1e), Laminazellen des Blattgrundes verlängert, 20–40 × 5–10 µm groß.

Diskussion. – Für eine Artzuordnung können diejenigen Arten der Gattung mit herablaufenden Blättern, gesäumten Blatträndern, mehrzelligen Blattzähnen und in der Blattspitze endender Rippe ausgeschlossen werden. Sehr ähnlich ist *R. hattorii* Nog. aus Neuguinea, die Pflanzen sind jedoch fast 2 cm groß und besitzen nahezu 2 mm lange Blätter sowie größere Laminazellen. Da lediglich in der Größe der Pflanzen und der Laminazellen deutliche Unterschiede bestehen, sind phylogenetische Beziehungen zwischen beiden Arten herstellbar.

Rhizogonium antiquum J.-P. Frahm & Preussing n. sp.

Taf. 2

Holotypus: SMNG/Geowissenschaftliche Sammlung Nr. 13233
Locus typicus: Braunkohlentagebau Berzdorf (Sachsen, Oberlausitz)
Stratum typicum: Mittelmiozän, Florenkomplex Kleinleipisch-Františkove Lázně.

Diagnose (lateinisch). – Ab aliis speciebus generis differt foliis elongate ovatis, valde limbatis, in parte superiore serratis, nervo percurrente.

Diagnose (deutsch). – Durch die verlängerten eiförmigen, deutlich gesäumten, im oberen Teil gesägten Blätter sowie die bis in die Blattspitze reichende Rippe von allen anderen Arten der Gattung abgrenzbar.

Beschreibung. – Fragment einer Moospflanze, 2,8 mm lang, mit sechs stark fragmentierten und vier nahezu vollständig erhaltenen Blättern (Taf. 2a). Blätter länglich-lanzettlich, apikal zugespitzt, am Grunde etwas kontrahiert, bis 0,78 mm lang und 0,24–0,28 mm breit (Taf. 2a, b); Blattrippe kräftig, in der Blattspitze endend (Taf. 2b, g); Blattrand durch drei bis vier Reihen verlängerter Zellen gesäumt, bis unterhalb der Blattmitte unregelmäßig gesägt (Taf. 2c, d, e), Blattspitze ungesäumt (Taf. 2b, g), äußere Saumzellen nahe des Blattgrundes verkürzt. Laminazellen glatt, irregulär vier- bis sechseckig bis rhombisch, etwas länger als breit, 15–30 × 7–15 µm groß (Taf. 2d, g), Laminazellen des Blattgrundes kaum verlängert (Taf. 2f).

Diskussion. – Keiner der sieben rezenten Vertreter der Gattung weist eine derartige Merkmalskombination auf. Diese Arten besitzen entweder keinen oder einen schwachen Blattsaum, längere Zähne am Blattsaum, eine austretende oder vor der Blattspitze verlöschende Rippe oder eine andere Blattform.

Ordnung Hypnales (M. Fleisch.) W. R. Buck & Vitt
Familie Plagiotheciaceae (Broth.) M. Fleisch.

Gattung *Isopterygiites* n. gen.

Diagnose (lateinisch). – Plantae regulariter pinnatae, ramis 4–5 mm longis, foliis circiter 1,1 mm longis, lanceolatis, enerviis, margine parce serratis, cellulis laminalibus elongate rhomboideis vel oblongis, apice proratis.

Diagnose (deutsch). – Pflanze regelmäßig gefiedert, Äste 4–5 mm lang, Blätter etwa 1,1 mm lang, lanzettlich, rippenlos, vereinzelt mit gesägtem Rand, Blattzellen verlängert-rhombisch bis linealisch, an der Spitze mit vorspringenden Zellecken.

Isopterygiites proratus J.-P. Frahm & Preussing n. gen. n. sp.
Taf. 3, Fig. 1–3

Holotypus: SMNG/Geowissenschaftliche Sammlung Nr. 13232/1 (Taf. 3, Fig. 1a–e)

Paratypen: SMNG/Geowissenschaftliche Sammlung Nr. 13232/2–4 (Taf. 3, Fig. 2a–b, 3)

Derivatio nominis: Der Name nimmt Bezug auf die papillös aufgebogenen oberen Zellecken.

Locus typicus: Braunkohlentagebau Berzdorf (Sachsen, Oberlausitz).

Stratum typicum: Mittelmiozän, Florenkomplex Kleinleipisch-Františkove Lázně.

Diagnose. – Siehe Gattungsdiagnose.

Beschreibung. – Drei Pflanzenfragmente von 2, 4 und 8 mm Länge sowie ein 4 mm langer Stämmchenrest mit fünf Seitenästen, diese regelmäßig fiedrig angeordnet, 4–5 mm lang (Taf. 3, Fig. 1a, 2a); z. T. fädige Pseudoparaphyllien an den Astprimordien sichtbar (Taf. 3, Fig. 1b, 3). Blätter lanzettlich, ganzrandig oder an der Spitze schwach gesägt, mit kurzer Doppelrippe, etwa 1,1 mm lang und 0,28–0,35 mm breit (Taf. 3, Fig. 1b, 1d, 1e). Obere Laminazellen verlängert-rhombisch bis linealisch, 25–50 × 5–10 µm groß, in der Blattspitze etwas kürzer und dickwandiger (Taf. 3, Fig. 1c, 1d); prorate (papillös aufgebogene) obere Zellecken regelmäßig vorhanden. Zwischen den Blättern z. T. fädige Cyanobakterien vorhanden.

Diskussion. – Aufgrund der kurzen Doppelrippe und der verlängerten Laminazellen der Blätter kommt eine Zuordnung zu den Plagiotheciaceae in Frage. Die geraden Blätter und besonders die fädigen Pseudoparaphyllien sprechen für eine enge Verwandtschaft zur Gattung *Isopterygium* Mitt. Für diese Gattung ungewöhnlich sind allerdings die proraten Zellecken und die regelmäßige Anordnung der Seitenäste, welche so bei einigen Sematophyllaceae anzutreffen sind. Die für diese Familie typischen Blattflügelzellen sind jedoch nicht erkennbar. Aufgrund der unsicheren Zuordnung wird die Art in eine neue Formgattung gestellt.

Familie Meteoriaceae KINDB.

Gattung *Meteorium* (BRID.) DOZY & MOLK.

Meteorium antiquum J.-P. FRAHM & PREUSSING n. sp.

Taf. 4, Fig. 1–2

Holotypus: SMNG/Geowissenschaftliche Sammlung Nr. 13234/10 (Taf. 4, Fig. 1a–c)
Paratypus: SMNG/Geowissenschaftliche Sammlung Nr. 13234/11 (Taf. 4, Fig. 2a–d)
Locus typicus: Tongrube Tetta-Buchholz (Sachsen, Oberlausitz).
Stratum typicum: Mittelmiozän, Florenkomplex Kleinleipisch-Františkove Lázně.

Diagnose (lateinisch). – Plantae foliis basi cordatis acuminatis, margine apicis irregulariter dentatis. Costa 4/5 folii occupante. Cellulae laminales ovatae vel rhomboideae, 8–20 × 5–10 µm, plurimum unipapillosae.

Diagnose (deutsch). – Blattgrund herzförmig, Blätter deutlich zugespitzt, Blattrand der Blattspitze unregelmäßig gezähnt, Blattrippe vier Fünftel der Blattlänge einnehmend. Blattzellen oval, 8–20 × 5–10 µm groß, meistens unipapillös.

Beschreibung. – Zwei Fragmente von 3,2 bzw. 2,2 mm Länge (Taf. 4, Fig. 1a, 2a) im selben Präparat mit *Andoa* cf. *berthelotiana*. Blätter stark fragmentiert, lanzettlich, aus breit eiförmiger Basis gleichmäßig lang zugespitzt, bis 0,65 mm lang und 0,15 mm breit (Taf. 4, Fig. 1a, 1b); Blattrippe kräftig, ungefähr vier Fünftel der Blattlänge erreichend, unterhalb der Blattspitze erlöschend (Taf. 4, Fig. 1b, 1c); Blattrand gesägt, an der Blattbasis kerbig, an der Blattspitze dornig (Taf. 4, Fig. 2b, 2d). Laminazellen oval bis rhombisch, ca. 8–20 × 5–10 µm groß, am Blattrand und in der Blattspitze verlängert, mit einer (selten zwei) deutlichen Papille über dem Lumen (Taf. 4, Fig. 2b, 2c, 2d).

Diskussion. – Hinsichtlich der Ausprägung der Blattrippe, des gezähnten Blattrandes sowie der oval geformten Laminazellen mit einer oder zwei Papillen gleichen die Pflanzen heutigen Vertretern der Meteoriaceae, am wahrscheinlichsten ist eine Zugehörigkeit zu *Meteorium*. Da die rezenten Arten dieser Gattung die beschriebene Merkmalskombination nicht aufweisen, erfolgt eine Neubeschreibung. Sehr ähnliche Arten, wie z. B. *M. papillarioides* NOG. aus China und Japan, unterscheiden sich durch ihre glatten Blattränder. Meteoriaceae kommen rezent in Europa nicht vor, sie sind typisch für temperate und tropisch-montane Regenwälder. Ein weiterer Vertreter der Familie (*Barbella* sp.) ist zweimal im Baltischen Bernstein gefunden worden (siehe FRAHM 2001a).

Familie Hypnaceae SCHIMP.

Gattung *Andoa* OCHYRA

Andoa cf. *berthelotiana* (MONT.) OCHYRA

Taf. 5, Fig. 1–6

Material: Neun kleine Pflanzenfragmente, mehr oder weniger gut erhalten, SMNG/Geowissenschaftliche Sammlung Nr. 13234/1–9.

Beschreibung. – Die Pflanzenfragmente sind 1 bis 4 mm lang. Blätter mit breitovalem Blattgrund, in eine feine lange Spitze verschmälert (Blattschnitt *Hylocomium*-artig), 0,8–1,3 mm lang und 0,23–0,45 mm breit (Taf. 5, Fig. 1, 2a, 3); Blattspitzen ein Drittel bis die Hälfte der Blattlänge einnehmend (Taf. 5, Fig. 1, 3); Blattrand unterschiedlich stark gezähnt, an der Spitze z. T. dornig (Taf. 5, Fig. 2b, 5, 6b); Blattrippe kurz zweischenkelig, vereinzelt so lang wie der Blattgrund. Laminazellen prosenchymatisch, 25–50 × 4–8 µm groß, zum Blattrand hin kürzer (Taf. 5, Fig. 2b); Zellwände im Gegensatz zu typischen Exemplaren von *Andoa berthelotiana* nur leicht verdickt und kaum getüpfelt, aber häufig mit den für die Art typischen deutlich proraten Zellecken.

Diskussion. – Die Merkmale der Pflanzenreste ähneln sehr denen von *Andoa berthelotiana*, einer Hypnaceae, welche rezent ausschließlich auf den Makaronesischen Inseln vorkommt. Das vorliegende Material stimmt mit den Abbildungen von *Andoa berthelotiana* von ABRAMOVA & ABRAMOV (1959) aus pliozänen Sedimenten des Kaukasus überein. Von rezenten Pflanzen unterscheiden sich die beschriebenen fossilen Pflanzen durch den bei einigen Blättern vorkommenden vollständig gezähnten Blattrand und den manchmal vorhandenen längeren Rippenschenkel (vgl. auch BROTHERUS 1925, Abb. 764). Daher bleibt die vorgenommene Zuordnung unsicher, möglicherweise handelt es sich nicht um *A. berthelotiana*, sondern um eine sehr ähnliche nahe verwandte Art oder einen direkten Vorfahren der heutigen Art.

Familie Neckeraceae SCHIMP.

Gattung *Homalia* BRID.

Homalia lusitanica SCHIMP.

Taf. 6

Material: Ein Pflanzenrest, SMNG/Geowissenschaftliche Sammlung Nr. 13235.

Beschreibung. – Das Fragment besteht aus einem 4,5 mm langen mittleren Teil von einem Ast oder Stämmchen mit 20 zum Teil erodierten Blättern (Taf. 6a). Blätter verflacht, scheinbar zweizeilig angeordnet, zungenförmig mit abgerundeten Spitzen, 1–1,2 mm lang und 0,22–0,26 mm breit (Taf. 6a, b, d); Blattrippe ungefähr drei Viertel der Blattlänge erreichend (Taf. 6b, d, e); Blattrand der Spitze kerbig gesägt (Taf. 6c, d). Laminazellen der unteren Blatthälfte gestreckt sechseckig, 50–60 × 10–15 µm groß (Taf. 6f), Laminazellen der oberen Blatthälfte kürzer, Laminazellen der Blattspitze rhombisch bis sechseckig, 15–25 × 10–15 µm groß (Taf. 6c).

Diskussion. – Der Moosrest zeigt die für die Gattung *Homalia* typische verflachte Beblätterung und ist nicht von der rezenten *Homalia lusitanica* zu unterscheiden, welche heute im Mittelmeergebiet und auf den Makaronesischen Inseln vorkommt. Diese Art wird für das Miozän von Frankreich (Jovet-Ast & Huard 1967) sowie für das Pliozän von Georgien (Abramova & Abramov 1959) angegeben.

4. Diskussion

Bemerkenswert ist, dass von den sechs nachgewiesenen Arten keine rezent in Mitteleuropa vorkommt und sich sogar vier ausgestorbene Arten darunter befinden. Von der im Neogen zu beobachtenden Zunahme holarktischer Laubmoossippen (Miller 1984, Frahm 2000) ist die Moosflora beider Fundstellen offenbar noch nicht betroffen. Die miozänen Fundstellen Mitteleuropas weisen in der Regel eine deutlich höhere Zahl holarktischer und rezent in Mitteleuropa vorkommender Arten oder zumindest Gattungen auf (z. B. Weyland 1937, Jovet-Ast & Huard 1967, Baranowska-Zarzycka 1975). Der ungewöhnlich hohe Anteil von bisher unbekannten Arten beider Lokalitäten ist für Fundstellen mit höherem geologischem Alter typisch. So zeigt die umfassende Bearbeitung der Lebermoose des eozänen Bernsteins Mitteleuropas, dass nur 3 der insgesamt 26 Arten heute noch vorkommen (Grolle & Meister 2004). Auch die entsprechenden Untersuchungen der Laubmoose zeigen eine nur geringe Übereinstimmung auf Artniveau (Frahm 2000, 2001a, 2004). Allerdings ist auf Gattungs- bzw. Familienebene die Übereinstimmung von den im Eozän und Neogen vorkommenden mit den gegenwärtigen Sippen sowohl bei den Leber- als auch den Laubmoosen hoch.

Die im Rahmen dieser Arbeit nachgewiesenen Arten geben Hinweise auf eine durch australasiatische *(Rhizogonium)*, mediterrane *(Andoa, Homalia)* und tropische *(Meteorium)*, also südliche bis südöstliche Florenelemente geprägte Moosflora an beiden Fundstellen. Auf eine hohe Affinität der eozänen baltischen Moosflora zur aktuellen Flora des temperaten bis tropischen Asiens weisen Untersuchungen sowohl an Laubmoosen (Frahm 2000) als auch Lebermoosen (Grolle & Meister 2004) im Bernstein hin. Die vorgestellten Moosarten fügen sich gut in das allgemeine mittelmiozäne Vegetationsbild Mitteleuropas ein, welches von warmtemperaten bis subtropischen, humiden Waldkomponenten geprägt wird (Mai 1995). Obwohl das neogene Klimaoptimum im späten Untermiozän bereits überschritten ist bzw. im Übergang von Unter- und Mittelmiozän von einer „Klimadepression“ ausgegangen werden muss (Czaja 2003), zeigt die Moosflora beider Fundstellen unter Berücksichtigung der beschriebenen Moosfunde keinerlei Einfluss borealer Elemente.

Die Nachweise von *Homalia lusitanica* und *Andoa berthelotiana* aus dem Neogen (Abramova & Abramov 1959, Jovet-Ast & Huard 1967, diese Arbeit) unterstützen die Aussage von Miller (1984), dass viele Moosarten jener Zeit auch gegenwärtig noch vorkommen. Es ist anzunehmen, dass die standörtlichen Bedingungen der heutigen Fundorte beider Arten sowohl im Mittelmeergebiet als auch auf den Makaronesischen Inseln den Bedingungen an den miozänen Fundorten ähnlich sind und die entsprechenden Moosarten eine viele Millionen Jahre lange Standortstreue aufweisen. Dies konnte auch bei Moosen im Baltischen Bernstein (Eozän) beobachtet werden, von denen ein Teil der heute noch existierenden Arten sowohl damals als auch aktuell in Eichen-Kiefernwäldern vorkommt (FRAHM 2004).

Bedeutend ist der Nachweis von zwei neuen Arten der Gattung *Rhizogonium*, von welcher bisher nur eine Art fossil aus Europa bekannt war. Vertreter dieser Gattung fehlen heute im holarktischen Bereich, ihre Hauptverbreitung liegt im australasiatischen Raum. Von dort haben sich die Arten bis nach Malaysia, Chile sowie Süd- und Mittelamerika ausgebreitet (FRAHM et al. 2003). Folglich war die Gattung mit mehreren Arten im Tertiär deutlich weiter nördlich verbreitet und ist in der Holarktis offenbar während der Eiszeiten erloschen. Parallelen sind diesbezüglich bei der Gattung *Echinodium* JUR. zu finden, die rezent in Australasien sowie disjunkt auf den Makaronesischen Inseln vorkommt. Die Gattung ist weiterhin im Miozän Europas aus Polen und Georgien bekannt. Das belegt, dass die Gattung im Miozän auf dem europäischen Festland vertreten war und, vermutlich durch den Einfluss der Eiszeiten, eine starke Arealrestriktion erfahren hat. Reliktär blieben Vorkommen mehrerer *Echinodium*-Arten auf den als Refugium der europäischen Tertiärflora bekannten Makaronesischen Inseln erhalten.

5. Literatur

ABRAMOVA, A. L. & ABRAMOV, I. I. (1959): Kimmerian mosses of the Duab River (Abkhazia). – Trudy Botanicesk Instituta Akademia Nauk SSSR, ser. 2, Sporovye Rasteniya, **12**: 301–359.

BARANOWSKA-ZARZYCKA, Z. (1975): The fossil flora of Turow near Bogatynia. Second part. Systematic description of plant remains (4). Musci. Neckeraceae, Amblystegiaceae, Brachytheciaceae, Entodonaceae. – Prace Muzeum Ziemi, **24**: 5–9.

BROTHERUS, V. F. (1925): Musci (Laubmoose) 2. Hälfte. – Die natürlichen Pflanzenfamilien, **11**: 542 S.; Leipzig (Wilhelm Engelmann).

CZAJA, A. (2003): Paläokarpologische Untersuchungen von Taphozönosen des Unter- und Mittelmiozäns aus dem Braunkohlentagebau Berzdorf/Oberlausitz (Sachsen). – Palaeontographica, Abteilung B, **265**: 1–148.

CZAJA, A. & BERNER, T. (1999): Tetta-Buchholz – eine neue Fundstelle tertiärer Pflanzenreste in der Oberlausitz. – Abhandlungen und Berichte des Naturkundemuseums Görlitz, **71** (2): 435–463.

FRAHM, J.-P. (2000): Neue Laubmoosfunde aus Baltischem Bernstein. – Cryptogamie, Bryologie, **21**: 121–132.

FRAHM, J.-P. (2001a): Neue Laubmoosfunde aus Sächsischem und Baltischem Bernstein. – Nova Hedwigia, **72**: 271–281.

FRAHM, J.-P. (2001b): Biologie der Moose. 357 S.; Heidelberg (Spektrum).

FRAHM, J.-P. (2004): A new contribution to the moss flora of Baltic and Saxon amber. – Review of Palaeobotany and Palynology, **129**: 81–101.

FRAHM, J.-P., BORCHARDT, P., SCHRAMM, M. & SONNTAG, M. (2003): Synopsis der Gattung *Rhizogonium* (Rhizogoniaceae). – Tropical Bryology, **24**: 129–137.

GOFFINET, B. & BUCK, W. R. (2004): Systematics of the Bryophyta (Mosses): From molecules to a revised classification. – In: GOFFINET, B., HOLLOWELL, V. & MAGILL, R. (Hrsg.): Molecular Systematics of Bryophytes: 205–239; St. Louis (Missouri Botanical Garden).

GROLLE, R. & MEISTER, K. (2004): The Liverworts in Baltic and Bitterfeld Amber. 91 S.; Jena (Weissdorn).

JOVET-AST, S. & HUARD, J. (1967): Mousses de la flore Néogène d'Arjuzanx (Landes). – Revue bryologique et lichénologique, **34**: 807–815.

MAI, D. H. (1964): Die Mastixioideen-Floren im Tertiär der Oberlausitz. – Paläontologische Abhandlungen, Abteilung B, **2**(1): 1–192.

MAI, D. H. (1995): Tertiäre Vegetationsgeschichte Europas. 691 S.; Jena, Stuttgart, New York (Gustav Fischer).

MAI, D. H. (2001): Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil III: Fundstellen und Paläobiologie. – Palaeontographica, Abteilung B, **258**: 1–85.

MILLER, N. G. (1984): Tertiary and Quaternary Fossils. – In: SCHUSTER, R. M. (Hrsg.): New manual of Bryology: 1194–1232; Nichinan (The Hattori Botanical Laboratory).

TIETZ, O. & CZAJA, A. (2004): Die Braunkohlenlagerstätte Berzdorf – Geologie, geologische Substrate und Paläobotanik. – Berichte der Naturforschenden Gesellschaft der Oberlausitz, **11**: 57–76.

WEYLAND, H. (1937): Beiträge zur Kenntnis der rheinischen Tertiärflora. II. Erste Ergänzungen und Berichtigungen zur Flora der Blätterkohle und des Polierschiefers von Rott im Siebengebirge. – Palaeontographica, Abteilung B, **83**: 67–122.

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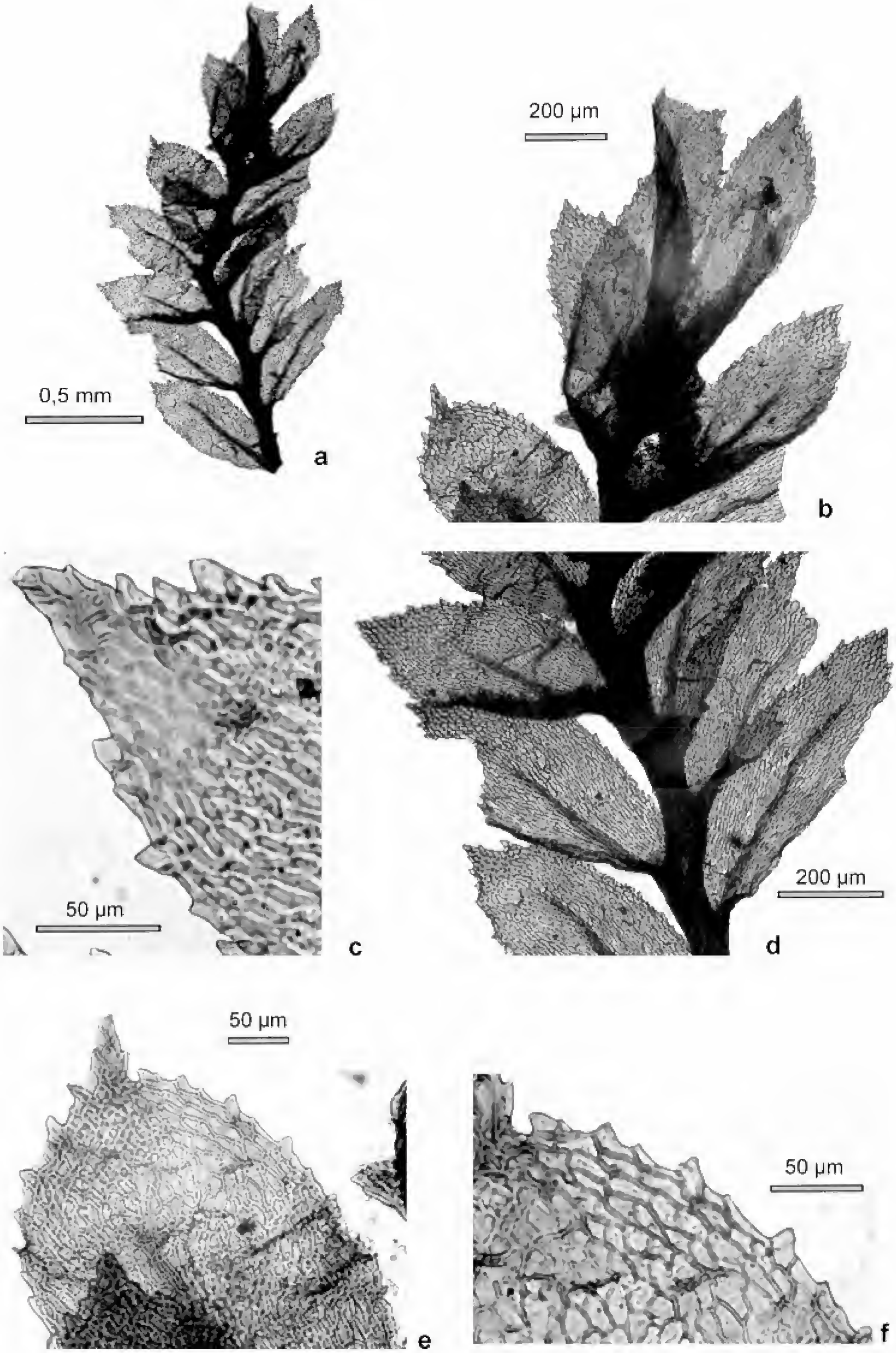
Tafel 1

Rhizogonium hattorioides n. sp., Holotypus, SMNG/Geowissenschaftliche Sammlung Nr. 13236;
a: Gesamtansicht des Pflanzenfragmentes; **b**: apikaler Teil der Pflanze; **c**: apikaler Teil eines Blattes; **d**: basaler Teil der Pflanze; **e**: Zellen im apikalen Teil eines Blattes; **f**: Detailansicht des Blattrandes.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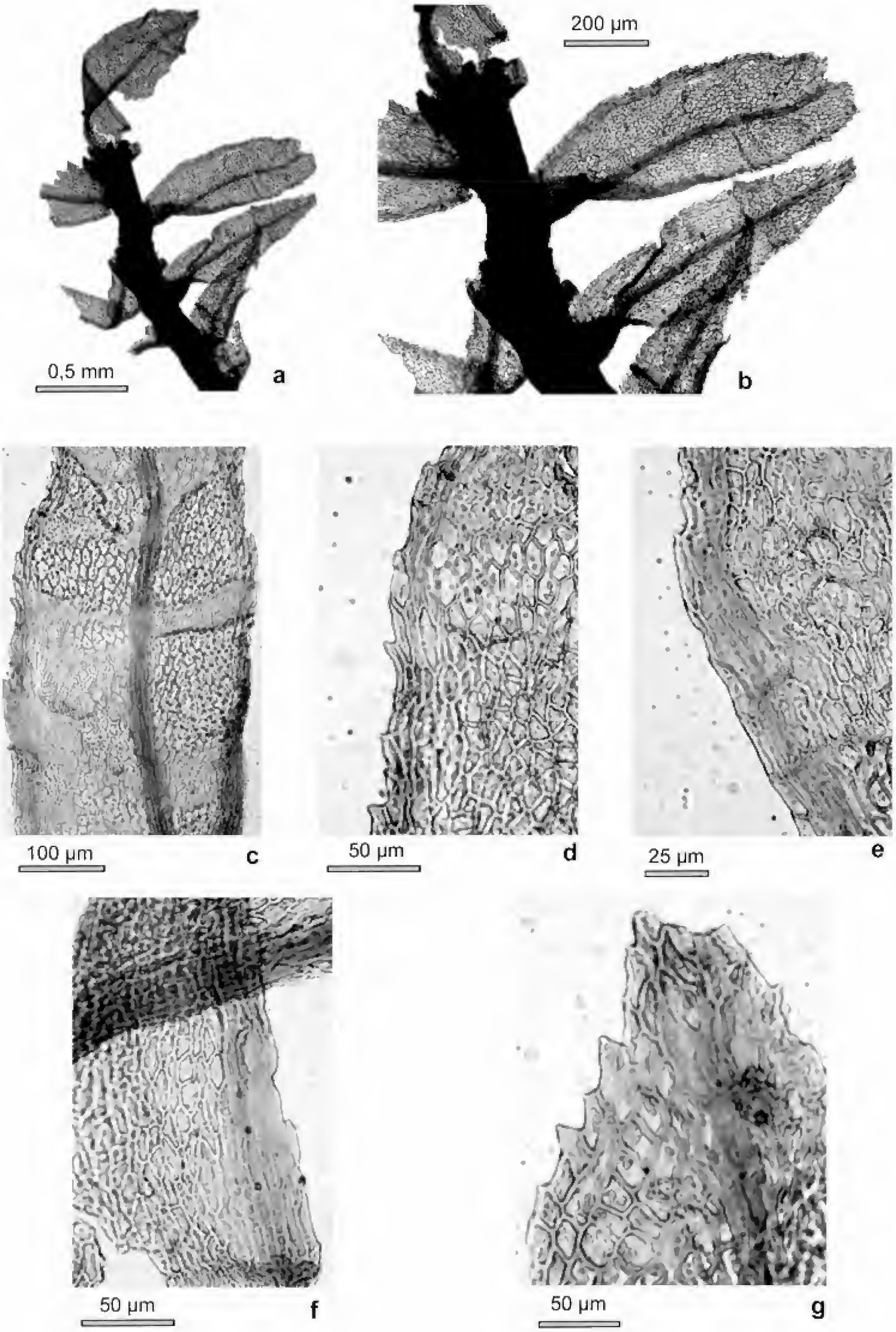
Tafel 2

Rhizogonium antiquum n. sp., Holotypus, SMNG/Geowissenschaftliche Sammlung Nr. 13233;
a: Gesamtansicht des Pflanzenfragmentes; **b**: Detailansicht des mittleren Teils der Pflanze; **c**: Ausschnitt aus dem mittleren Teil eines Blattes; **d**: Ausschnitt aus dem oberen Rand eines Blattes; **e**: Ausschnitt aus dem unteren Rand eines Blattes; **f**: Ausschnitt aus dem Blattgrund; **g**: Detailansicht der Blattspitze.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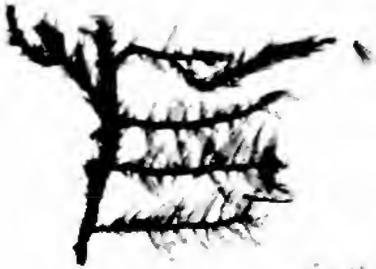
Tafel 3

Isopterygiites proratus n. gen. n. sp.

Fig. 1. Größtes erhaltenes Pflanzenfragment mit Fiederung, Holotypus, SMNG/Geowissenschaftliche Sammlung Nr. 13232/1; **a**: Gesamtansicht; **b**: Detailansicht mit Pseudoparaphyllien am Astprimordium; **c**: Apikalteil eines Blattes; **d**: Detailansicht einer Blattspitze; **e**: Detailansicht einer Blattspitze.

Fig. 2. Pflanzenfragment, Paratypus, SMNG/Geowissenschaftliche Sammlung Nr. 13232/2; **a**: Gesamtansicht; **b**: Detailansicht.

Fig. 3. Einzelnes Pseudoparaphyllium in Blattachsel, Paratypus, SMNG/Geowissenschaftliche Sammlung Nr. 13232/3.



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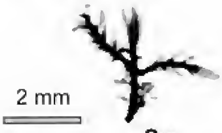

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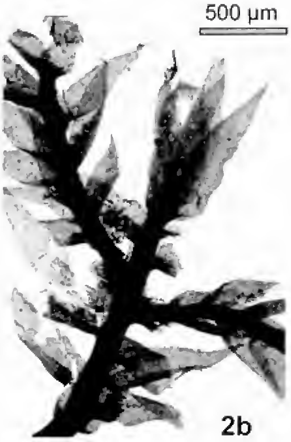

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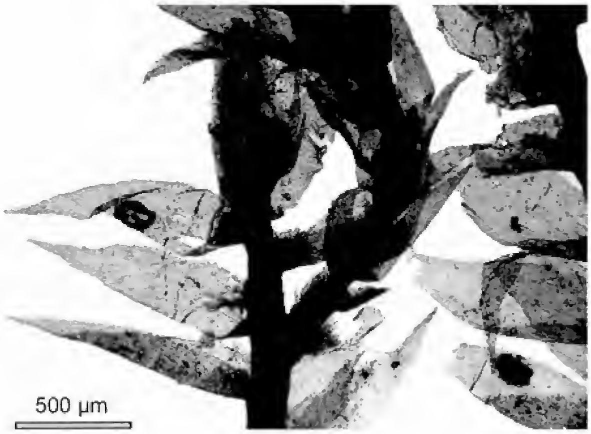

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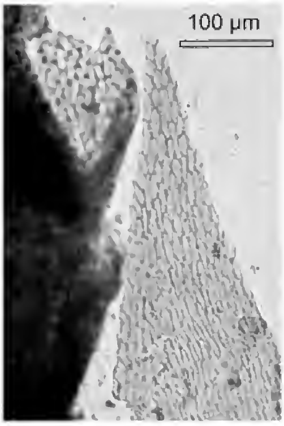

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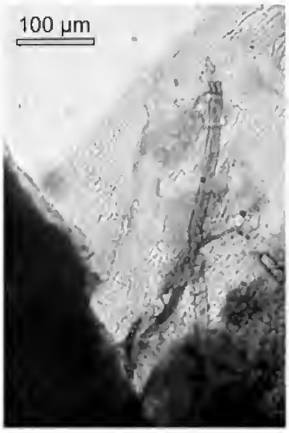

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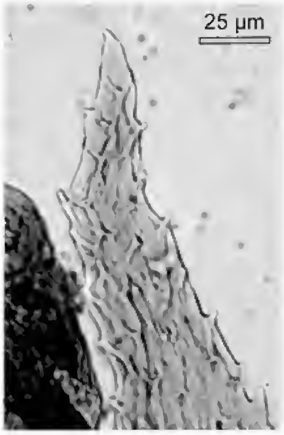

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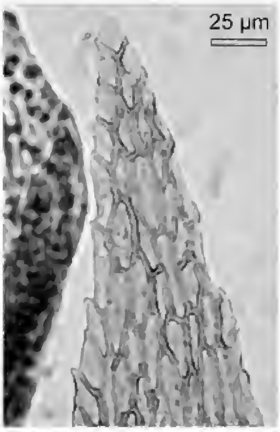


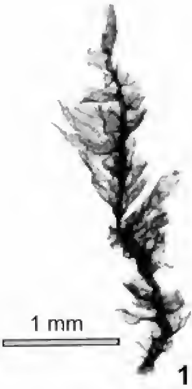
1d

Tafel 4

Meteorium antiquum n. sp.

Fig. 1. Pflanzenfragment, Holotypus, SMNG/Geowissenschaftliche Sammlung Nr. 13234/10; **a**: Gesamtansicht; **b**: Ausschnitt mit gut erhaltenen Blättern; **c**: Detailansicht der Blattspitze mit endender Blattrippe.

Fig. 2. Pflanzenfragment, Paratypus, SMNG/Geowissenschaftliche Sammlung Nr. 13234/11; **a**: Gesamtansicht; **b**: Detailansicht einer Blattspitze; **c**: Detailansicht derselben Blattspitze wie Fig. 2b mit Zellen; **d**: Mittlerer Teil eines Blattes mit Zellen.



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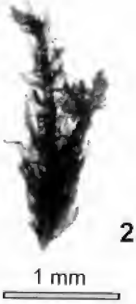

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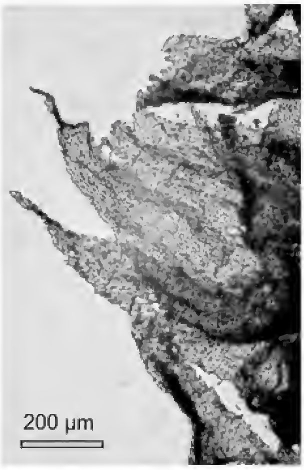

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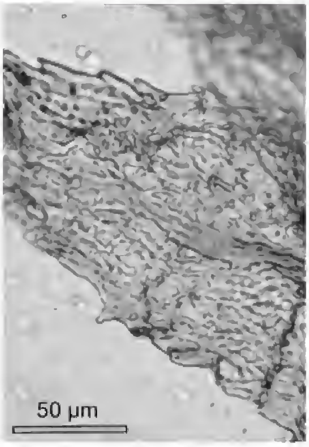

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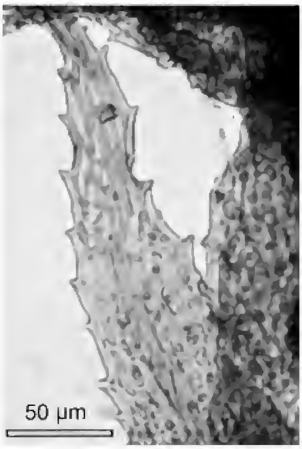

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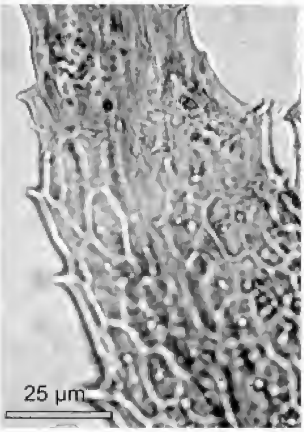

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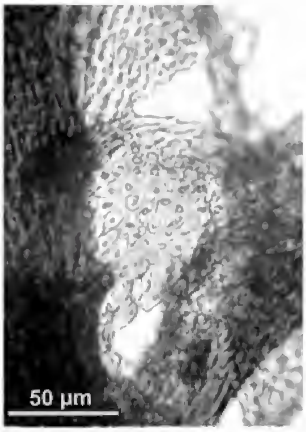


2d

Tafel 5

Andoa cf. *berthelotiana* (MONT.) OCHYRA

Fig. 1. Pflanzenfragment, SMNG/Geowissenschaftliche Sammlung Nr. 13234/1.

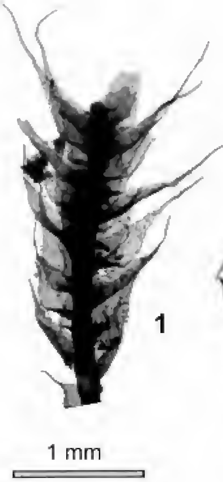
Fig. 2. Pflanzenfragment, SMNG/Geowissenschaftliche Sammlung Nr. 13234/2; **a**: Gesamtansicht; **b**: Ausschnitt aus dem oberen Blattbereich.

Fig. 3. Pflanzenfragment, Gesamtansicht, SMNG/Geowissenschaftliche Sammlung Nr. 13234/3.

Fig. 4. Pflanzenfragment, Gesamtansicht, SMNG/Geowissenschaftliche Sammlung Nr. 13234/4.

Fig. 5. Pflanzenfragment, Spitzen von 3 Blättern, SMNG/Geowissenschaftliche Sammlung Nr. 13234/5.

Fig. 6. Pflanzenfragment, SMNG/Geowissenschaftliche Sammlung Nr. 13234/6; **a**: Detailansicht einer Blattspitze mit Zellen; **b**: Detailansicht eines Blattes mit abgebrochener Spitze.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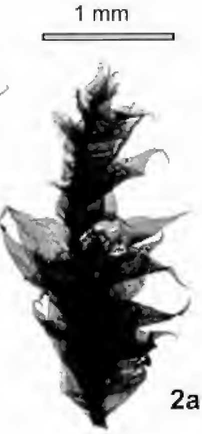
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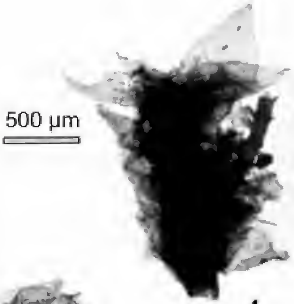
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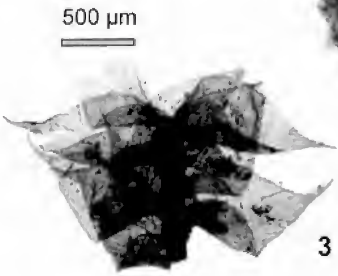
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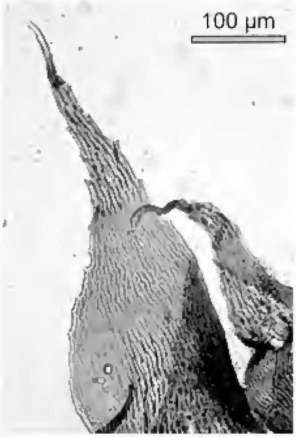
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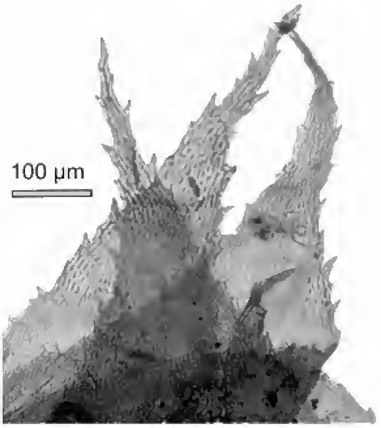
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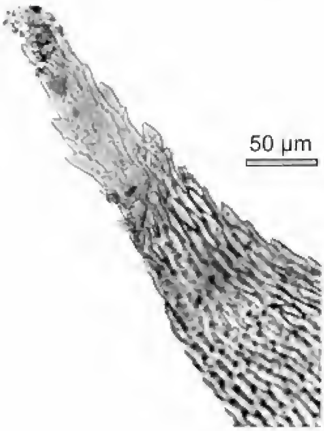
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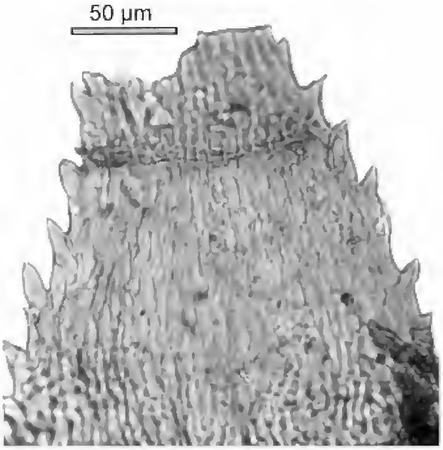
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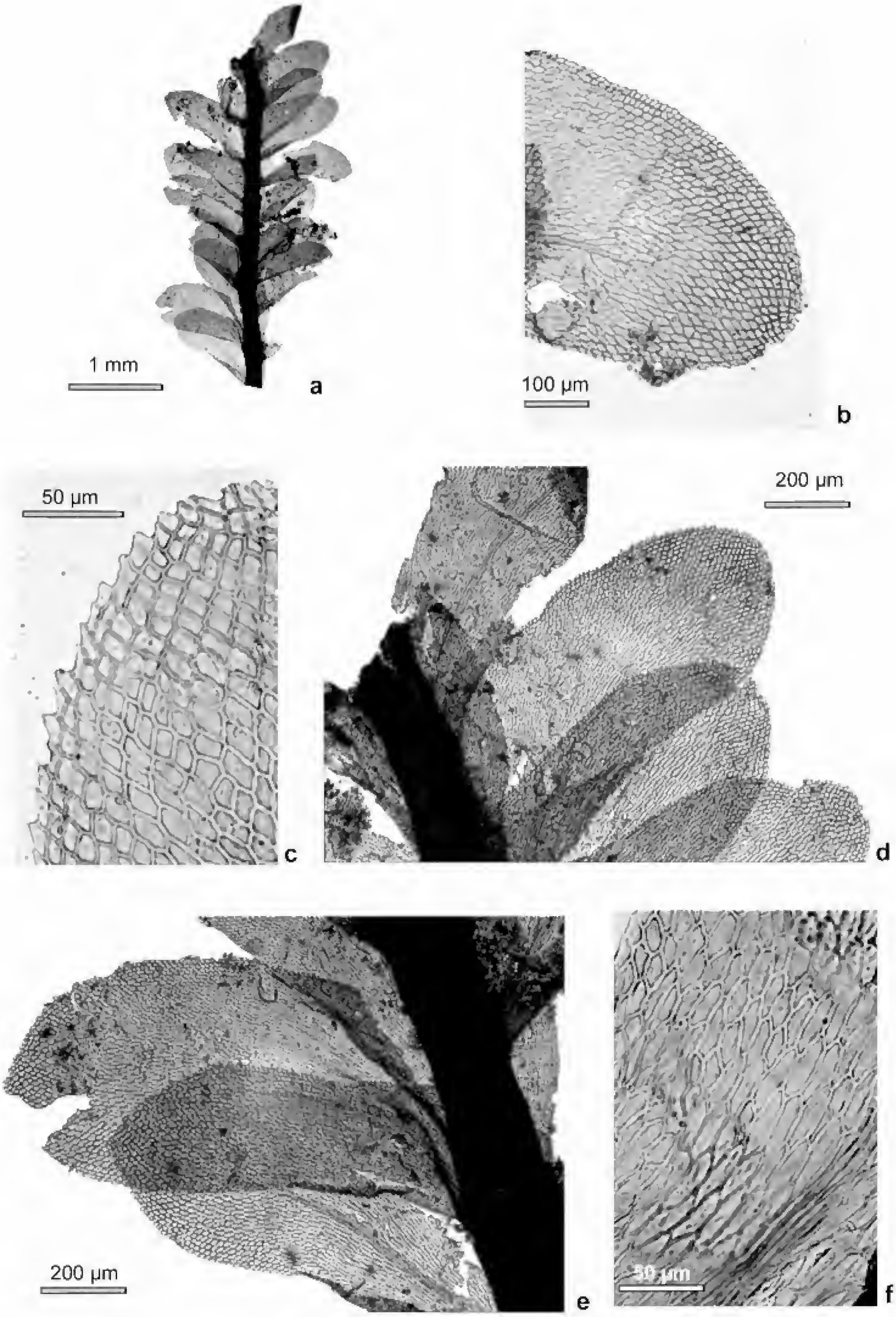
Tafel 6

Homalia lusitanica Schimp., SMNG/Geowissenschaftliche Sammlung Nr. 13235; **a**: Gesamtansicht des Pflanzenfragmentes; **b**: obere Hälfte eines Blattes; **c**: Detailansicht von Blattspitze und Randbereich mit Zellen; **d**: Ausschnitt des apikalen Teiles der Pflanze; **e**: Ausschnitt des basalen Teiles der Pflanze; **f**: Detailansicht vom oberen Bereich des Blattgrundes mit Blattrippe.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The Ovale Zone (Lower Bajocian, Middle Jurassic) at Little Down Wood (Dundry Hill, Somerset, SW England)

VOLKER DIETZE, ROBERT B. CHANDLER & JOHN H. CALLOMON

Abstract

A new section is described through the Ovale Bed in the Middle Inferior Oolite at the western end of the outlier on Dundry Hill, south of Bristol. It provides new insights into the biostratigraphy of the ammonites of the Ovale Zone of the Lower Bajocian, still one of the least well-known parts of that Stage and of its succession of faunal horizons. The lower part of the bed is assigned to the horizon Bj-5, that of *Witchellia romanoides* (DOUVILLÉ). The upper part represents at least in part the former horizon Bj-6, that of '*Sonninia*' *ovalis* sensu BUCKMAN, which is in need of revision. Some of the more important ammonites are illustrated, including the lectotypes, here designated, of '*Ludwigia*' *romanoides* DOUVILLÉ and *Witchellia sayni* HAUG. A neotype is designated for *Strigoceras compressum* BUCKMAN, whose original type series came from the Ovale Zone of Dundry.

Keywords: Ammonites, biostratigraphy, Dundry, Inferior Oolite, Jurassic, Lower Bajocian.

Zusammenfassung

Vom Dundry Hill südlich Bristol (Somerset, Südwest-England) wird ein neuer Aufschluss im Ovale Bed des Middle Inferior Oolite beschrieben. Dieser erlaubt neue Einblicke in die Feinstratigraphie der bisher nur unzureichend bekannten Ovale Zone des Unter-Bajociums. Der untere Teil des Ovale Bed kann zum Ammoniten-Faunenhorizont der *Witchellia romanoides* (Bj-5, Ovale-Zone, Unter-Bajocium) gestellt werden. Der obere Teil enthält zumindest auch den revisionsbedürftigen vormaligen Ammoniten-Faunenhorizont Bj-6 („*Sonninia*“ *ovalis* sensu BUCKMAN). Einige der wichtigeren Ammoniten werden beschrieben und abgebildet, einschließlich der hier designierten Lectotypen von „*Ludwigia*“ *romanoides* DOUVILLÉ und *Witchellia sayni* HAUG. Für *Strigoceras compressum* BUCKMAN, dessen Typen-Serie aus der Ovale-Zone von Dundry stammt, wird ein Neotypus designiert.

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1. Introduction

The outcrops of Inferior Oolite (Aalenian and Bajocian Stages) on Dundry Hill (near Bristol, Somerset) are of exceptional importance for Middle Jurassic stratigraphy more generally, especially for that of the Lower Bajocian. Fossils from the most famous localities (e.g. South Main Road Quarry and North Main Road Quarry) are to be found in nearly every museum collection. Descriptions of the sections and fossils occur in many classical works (for details see BUCKMAN & WILSON (1896) and PARSONS (1979)), going back to the days of WILLIAM SMITH. The lectotype of the index-species of the Lower Bajocian Laeviuscula Zone, *Ammonites laeviusculus*, comes from Dundry Hill as does the lectotype of *Ammonites sowerbyi*, index-species of the former Sowerby Zone.

The first modern description of the stratigraphy of Dundry Hill is by BUCKMAN & WILSON (1896), who described the available sections very carefully bed by bed. They were classified in terms of the scheme of 'hemerae' ('moments', marking 'the acmes of ammonite species') introduced in his classical publication of 1893 by BUCKMAN, and thence correlated with the rocks of the Cotswolds, Dorset and Somerset that had already been described in this way. Subsequent detailed investigations were undertaken by PARSONS (1974, 1979, 1980) who classified and resolved the Inferior Oolite of Dundry in terms of the then standard Jurassic chronostratigraphical zonation taken down to the level of Zones and Subzones. The first interpretation of the succession at the highest achievable biostratigraphical resolution, that of ammonite faunal horizons, was given by CALLOMON & CHANDLER (1990); and the biostratigraphy of the particular case of the South Main Road Quarry (Du-SMR) was described in detail by CHANDLER et al. (2006). The focus was on the Laeviuscula and Sauzei Zones, especially on the boundary between them, but there remained some major uncertainties in the interpretation of the beds below, those of the Ovale Zone. These are encompassed by the so-called Ovale Bed (sensu PARSONS), and the purpose here is to describe in detail the ammonites and stratigraphy of this bed at a new locality, Little Down Wood (Du-LDW), which lies 2.5 km NW of Du-SMR.

Figured material is from collections made by the authors and supported by additional material collected by one of us (JHC) in the 1970s. Photographs are by RBC. Specimens will be deposited in the Sedgwick Museum (Cambridge).

Abbreviations

Du-LDW	Dundry, Little Down Wood
Du-SMR	Dundry, South Main Road (CHANDLER et al. 2006)
+	single specimen
++	2 or 3 specimens
+++	4 or more specimens
[m]	microconch ammonite species
[M]	macroconch ammonite species
*	an asterisk before the name of a species indicates the type species of its genus
TA	BUCKMAN's (1909–1930) Type Ammonites
BSPG	Bayerische Staatssammlung für Paläontologie und Geologie München, Germany
SM	Sedgwick Museum, Cambridge, United Kingdom
STL	Dépt. des Sciences de la Terre, geological collections, Université Claude Bernard, Lyon, France

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2. The section at Dundry, Little Down Wood

The new section lies immediately above an old quarry, at ST 549_2 675_0, about 12 m east of BUCKMAN & WILSON's "Section I. Western End, near Castle Farm" (1896) and also close to the "Grove Farm" section of PARSONS (1979). Following trial excavations by hand we opened the new section in the early summer of 2006 using a machine. Due to restricted time and the position of the site being close to a cultivated area, we focused our attention on the top beds beneath the prominent regional erosion plane that marks the "Vesulian transgression" and the boundary between the Middle and Upper Inferior Oolite (Lower and Upper Bajocian respectively). The beds and the levels of ammonites within them are recorded as measurements downwards from the surface of the erosion plane taken as 0 cm. The section is described from above. It is shown diagrammatically in Fig. 1. The numbering of the beds is taken over from the generalized succession of PARSONS (1979). Names of ammonites are in a morphospecific sense, discussed further below.

Upper Inferior Oolite, Dundry Freestone (seen about 1 m)
(Parkinsoni Zone, Acris and ?Truellei Subzones)

Limestone, soft, marly, massive freestone showing little sign of bedding; very sparsely fossiliferous. Maes Knoll Conglomerate at the base, thickening up to 0.15 m, with small limonitic pebbles in the lower part (not investigated in detail). Rare specimens of the ammonite *Parkinsonia rarecostata* in the Maes Knoll Conglomerate show its equivalence to the Astarte Bed of Dorset, indicating the Acris Sub-

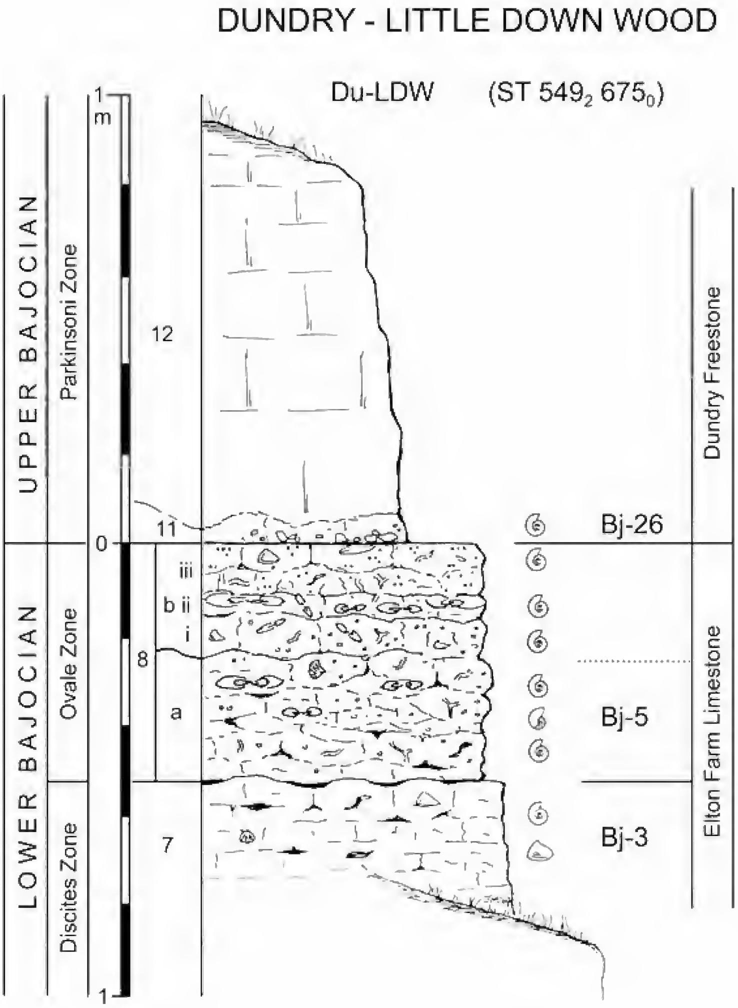
DUNDRY - LITTLE DOWN WOOD
Du-LDW (ST 549_2 675_0)
UPPER BAJOCIAN
LOWER BAJOCIAN
Parkinsoni Zone
Ovale Zone
Discites Zone
1
m
0
1
12
11
iii
b ii
i
8
a
7
Bj-26
Bj-5
Bj-3
Dundry Freestone
Elton Farm Limestone

Fig. 1. Section at Dundry, Little Down Wood.

zone of the Parkinsoni Zone (Upper Bajocian). A loose fragmentary specimen of *P. parkinsoni* either from the Maes Knoll Conglomerate or the Freestone above is typical of the Truellei Subzone of the Parkinsoni Zone.

– Sharp boundary, marked by the very flat Vesulian erosion-plane, with encrustations of small oysters.

Middle Inferior Oolite, Elton Farm Limestone (seen about 0.80 m)
(Ovale and Discites Zones)

– Bed 8 (= *ovalis* bed of Parsons)
(Ovale Zone)

Limestone, hard, sparsely finely ironshot oosparitic in the upper part, oolitic with sparse cream ooliths lower down, intensely bioturbated and burrowed, the burrows mostly of *Thalassinoides* type. Subdivisible with difficulty into courses with undulating boundaries but no changes in lithology, weathered locally into pockets or lenticles of limonitic marl. Variably fossiliferous, notably with large bivalves, both of entire endofaunal burrowers and thick-shelled ectofauna, the oysters and pectinids with test preserved. Large ammonites, especially *Fissilobiceras*, with body-chambers preserved, mainly lying flat at random levels throughout the bed but particularly common at –0.10/–0.15 m; small ammonites preserved at all angles, tending to be concentrated mainly at two levels (–0.10/–0.15 and –0.30 m), microconchs sometimes with lappets preserved. Many rotted patches due to superficial weathering. Nautiloids are represented by *Cenoceras obesum* (J. Sowerby), belemnites are abundant and there are small solitary corals.

The bed yields a rich fauna of well-preserved bivalves, the calcitic forms with test preserved. Prominent among them are:

Plagiostoma hersilia (d'Orbigny) [up to 17 cm in diameter]
Ctenostreon pectiniformis (Schlotheim)
Coelastarte excavata (J. Sowerby) [= *Astarte obliqua* auctt.]
Trigonia costata J. de C. Sowerby
T. cf. *spinulosa* Young & Bird
Gervillella sp.
'*Ostrea*' sp.
Pholadomya cf. *lirata* (J. Sowerby)
Ph. deltoidea (J. Sowerby)
Ph. fidicula (J. Sowerby)
Pleuromya uniformis (J. Sowerby)

– Bed 8 b(iii) (0.00 m to –0.10 m)

The bed is heavily bioturbated. Ammonites sparse, mostly fragmentary and distorted.

Ammonite fauna:

Witchellia romanoides (Douvillé) (++) and sp. aff. (+++) [M]
W. pavimentaria (Buckman) [M] (+)
W. patefactor Buckman [M] (+)
Sonninia (Euhoploceras) sp. [M] (+)
Dundryites albidus Buckman [M] (++)
Emileia sp. [M] (+)

– Bed 8 b(ii) (–0.10 m to –0.15 m)

A level with many large ammonites, up to 0.30 m in diameter, lying flat, associated with small ammonites lying at all angles. Many of the small ammonites well preserved with sparitic phragmocones and shell and ornament intact, indicating minimal exposure before burial; few shells however complete, often broken off near the last septa. Detached fragments not preserved with counterparts, so some post-mortal destruction and movement is evident. Larger specimens, mainly bodychamber fragments, invariably preserved as internal moulds. Broken edges of the fragments wel-

ded into the matrix, suggesting considerable re-exhumation and destruction prior to final burial. Phragmocones of larger ammonites sometimes partially or completely replaced by limonite, the nuclei lost. Some of the specimens are heavily bored.
Ammonite fauna:
Witchellia romanoides (Douvillé) [M] (+++) (Pl. 4, Fig. 3)
W. cf. *sayni* Haug [M] (++)
W. connata (Buckman) [M] (++) (Fig. 3c–d)
W. cf. *patefactor* Buckman [M] (+) (Pl. 7, Fig. 1)
W. pavimentaria Buckman [M] (+)
Pelekodites pelekus Buckman [m] (+) (Fig. 4a–b)
P. aff. *minimus* (Hiltermann) [m] (+) (Fig. 4c)
Sonninia aff. *haugi* Gillet [sp. nov.] [?m] (++)
S. (Euhoploceras) pseudotrigonata Maubeuge [M] (+) (Pl. 2, Fig. 2)
S. (E.) aff. *adicra* (Waagen) [M] (+) (Pl. 2, Fig. 1)
S. (E.) spp. [M] (+)
Dundryites aff. *albidus* Buckman [M] (++) (Pl. 3, Fig. 1)
Fissilobiceras fissilobatum (Waagen) [M] (++)
F. ovale (Quenstedt) [M] (+++)
?*Shirbuirnia* sp. (cf. Callomon & Chandler 1990, pl. 1, fig. 1) [M] (+)
"*Emileites*" [gen. nov.] *liebi* (Maubeuge) [M] (+++)
"*Trilobiticeras*" [gen. nov.] *cricki* Parsons [m] (+++) (Pl. 9, Fig. 7–8)
Emileia (Emileia) dundriensis Callomon & Chanlder. [M] (++) (Pl. 11, Fig. 1)
Emileia (Emileites) malenotata (Buckman) [M] (++) (Pl. 9, Fig. 1–2)
Otoites tumulosus Westermann [m] (++) (Pl. 10, Fig. 3)
O. douvillei Parsons [m] (+) (Pl. 10, Fig. 2)
Stephanoceras aff. *richardsoni* (Dietze et al.) [sp. nov.] [M] (+) (Fig. 6)
Bradfordia cf. *praeradiata* (Douvillé) [M] (++) (Fig. 7a–b)
B. cf. *costidensa* Imlay [M] (++) (Fig. 7h)
Strigoceras compressum Buckman [M] (+) (Fig. 5c)
S. strigifer (Buckman) [M] (+) (Fig. 5a–b)
Hebetoxyites hebes Buckman [?M] (++) (Fig. 7d, i)
by preservation from this level:
Emileia (E.) aff. *dundriensis* Callomon & Chandler [M] (+) (Pl. 10, Fig. 1; Pl. 11, Fig. 2)

– Bed 8 b(i) (–0.15 m to about –0.20/–0.25 m)

Lithology as above, ammonites throughout but less common in the lower part.
Ammonite fauna:
Witchellia romanoides (Douvillé) [M] (+++) (Pl. 4, Fig. 4)
W. cf. *jugifera* (Waagen) [M] (+)
W. connata (Buckman) [M] (+)
W. cf. *zugophora* (Buckman) [M] (+) (Pl. 6, Fig. 3)
Pelekodites pelekus Buckman [m] (+) (Fig. 4f–g)
P. aff. *minimus* (Hiltermann) [m] (+)
P. cf. *aurifer* (Buckman) [m] (+) (Fig. 4h–i)
Sonninia aff. *haugi* Gillet [?m] (++) (Pl. 1, Fig. 1)
Sonninia (Euhoploceras) pseudotrigonata Maubeuge [M] (+)
S. (E.) spp. [M] (++)
Dundryites albidus Buckman [M] (+) (Pl. 3, Fig. 2)
Fissilobiceras fissilobatum (Waagen) [M] (++)
F. ovale (Quenstedt) [M] (+++) (Pl. 8, Fig. 1)
"*Emileites*" [gen. nov.] *liebi* (Maubeuge) [M] (+++) (Pl. 9, Fig. 3–4)
"*Trilobiticeras*" [gen. nov.] *cricki* Parsons [m] (+++)
Otoites tumulosus Westermann [m] (++)
Bradfordia praeradiata (Douvillé) [M] (+)
Lissoceras? cf. *semicostulatum* Buckman [M] (+) (Fig. 7c)

– Beds 8 b and 8 a separable when weathered, boundary undulating between –0.20 to –0.25 m below the top of the erosion plane, but not marked by significant changes in lithology.

– Bed 8 a (–0.20/–0.25 m to –0.50/–0.55 m)
(*Witchellia romanoides* ammonite faunal horizon (Bj-5))

The bulk of the ammonites, mostly small, concentrated at about –0.30 m, few occurring lower. The limestone is cream to pale brown with small nut-brown ooliths, sometimes harder than the bed above, or weathered to marl with ochreous lenticles and limonitic clay in the lower part.

Ammonite fauna:

Witchellia romanoides (Douvillé) [M] (+++) (Pl. 4, Fig. 1)
W. cf. *sayni* Haug [M] (+++) (Pl. 6, Fig. 2)
W. cf. *jugifera* (Waagen) [M] (++) (Pl. 5, Fig. 2)
Pelekodites pelekus Buckman [m] (+) (Fig. 4d–e)
P. aff. *minimus* (Hiltermann) [m] (+)
P. cf. *aurifer* (Buckman) [m] (+) (Fig. 4j–k)
Sonninia (Euhoploceras) cf. *subdecorata* Buckman [m] (++) (Pl. 1, Fig. 2–3)
S. (E.) spp. [M] (+)
Dundryites albidus Buckman [M] (++)
Fissilobiceras fissilobatum (Waagen) [M] (++)
F. ovale (Quenstedt) [M] (++) (Pl. 8, Fig. 2)
"*Emileites*" [gen. nov.] *liebi* (Maubeuge) [M] (+++) (Pl. 9, Fig. 5)
"*Trilobiticeras*" [gen. nov.] *cricki* Parsons [m] (+++) (Pl. 9, Fig. 6)
Oppelia? sp. [M] (+) (Fig. 7f–g)
Strigoceras compressum Buckman [M] (+) (Fig. 5d)

– inconspicuous undulating parting, change of lithology

– Bed 7 (= Bivalve bed partim of Parsons) (seen –0.50/–0.55 m to –0.70/–0.80 m)
(Discites Zone, *Hyperlioceras subsectum* ammonite faunal horizon (Bj-3))

The lowest bed exposed but not more fully investigated: a very hard, more densely sparitic limestone weathering in large blocks with pockets and lenticles of ochreous limonitic clay. Sparsely fossiliferous, containing large bivalves and very rare ammonites.

Ammonite fauna:

Hyperlioceras subsectum Buckman [M] (++)
Sonninia (Euhoploceras) biplicata Buckman [M] (+)
S. (E.) modesta Buckman [M] (+)

Lower part of the bed not seen. According to Parsons (1979) the bed continues downwards at Grove Farm, where he recorded a thickness of 0.43 m. Neither Buckman & Wilson (1896) nor Parsons (1979) recorded any ammonites from this part of the succession.

3. Bio- and chronostratigraphy

3.1. General remarks

In his famous account of the Bajocian of the Sherborne district Buckman (1893) introduced his *Witchelliae* hemera for all the strata between those of an upper *Sauzei* hemera and a lower *Discitae* hemera. The beds assigned by him to his *Witchelliae* hemera at Dundry (his section XVIII, outline section of the top of Dundry Hill) consisted of "White Ironshot" and included the strata revised here.

By 1896 Buckman & Wilson had refined this part of the succession at Dundry (their tab. IV). The interval between *Sauzei* and *Discitae* hemerae was now subdivided into two: the *Witchelliae* hemera for the upper part, represented by 'The Upper White Ironshot', and a *Sonniniae* hemera for the lower part, 'The Lower White Ironshot – the *fissilobata-ovalis* horizon'. These ammonites, then still assigned to the genus *Sonninia*, are today placed in *Fissilobiceras*. In their section I (Western End, near Castle Farm, p. 676), they assigned the 43 cm of strata below the erosion plane, the 'Lower White Ironshot' – their beds 4–8 (p. 678), matching closely our bed 8 – to this *Sonniniae* hemera. The higher beds of the restricted *Witchelliae* hemera were recognized to have been cut out by erosion at the western end of the hill.

In the final hemeral table in Buckman's Type Ammonites (Davies 1930), the *Sonniniae* hemera was replaced through further subdivision, in ascending order, by the *Bradfordia*, *ovalis* and *fissilobatum* hemerae.

The next step after a long interval was taken by Parsons (1974, 1977, 1979). He reviewed the somewhat confused evolution of the White Ironshot of Dundry (1979, tab. 3) and abandoned the 'Lower Ironshot' in favour of what had become known as the '*ovalis* bed', bed 8 in his general classification. At Grove Farm, close to our Du-LDW, he could subdivide the bed (0.48 m) by lithology into two, beds 8a and 8b respectively. He was not able to separate their faunas, but most of the recorded ammonites came from a level at about 0.10 m below the top of the bed. At nearby Barns Batch Spinney, the bed could also be subdivided and the ammonite faunas were mainly concentrated at –0.10/–0.15 and –0.25 m below the top of the bed. A third component, bed 8c, was inserted by Chandler et al. (2006) in the section at South Main Road (Du-SMR).

Lastly, Callomon & Chandler (1990) revived the concept of the ammonite hemerae of Buckman in terms of their rock equivalents, their faunal horizons, basic biostratigraphical units defined by characteristic fossil assemblages distinguishable from their neighbours in succession by evolutionary, genotypic changes in phenotypic morphology. The number of such biohorizons is unlimited, depending on the state of knowledge, and increases by insertion as new discoveries are made. In the Inferior Oolite, some 26 such faunal horizons have currently been characterized in the Lower Bajocian, labelled symbolically in the range Bj-1 to Bj-19 and named after their most characteristic species. Those up to and including the Sauzei Zone are shown in Fig. 2, taken from a recent revision by Chandler et al. (2006, Du-SMR). Of these, the only ones relevant here are in the range Bj-3 (upper Discites Zone) to Bj-7a, b, Ovale to basal Laeviuscula Zones.

It is those of the Ovale Zone that have so far been least well characterized and it is to their knowledge that the new collections from Du-LDW make a contribution. They are discussed further below.

3.2. The ammonite succession

The lists of species that have been collected are given above in the description of the section.

What follows is an analysis of the assemblages, their classification in the framework of faunal horizons and their correlations with successions elsewhere. Individual taxa are more extensively annotated in § 4 below.

Zone	Subzone	Ammonite faunal horizons
Sauzei		Bj-12 *Stephanoceras rhytum*
		Bj-11b *Nannina evoluta*
		Bj-11a *Stephanoceras kalum*
Laeviuscula	Laeviuscula	Bj-10b *Sonninia micracanthica*
		Bj-10a *Witchellia spinifera*
		Bj-9 *Witchellia rubra*
	Trigonalis	Bj-8b *Shirbuirnia trigonalis*
		Bj-8a *Euhoploceras nodatipingue*
		Bj-7b *Witchellia pseudoromanoides*
Ovale		Bj-7a *Witchellia gelasina*
		Bj-6c *Witchellia pseudoromani* MS
		Bj-6b *Shirbuirnia gingensis*
		Bj-6a *Witchellia zugophora*
		Bj-5 *Witchellia romanoides*
		Bj-4 *Bradfordia inclusa*
Discites		Bj-3 *Hyperlioceras subsectum*
		Bj-2b *Hyperlioceras rudidiscites*
		Bj-2a *Hyperlioceras walkeri*
		Bj-1 *Hyperlioceras politum*

Fig. 2. The ammonite faunal horizons in the English Lower Bajocian up to and including the Sauzei Zone (from CHANDLER et al. 2006).

3.2.1. Lower Bajocian, Discites Zone

Bed 7: Faunal horizon Bj-3, *Hyperlioceras subsectum*
A few new specimens of *Hyperlioceras* of the *H. subsectum*-group and fragments

of *Sonninia (Euhoploceras)* sp. support earlier finds elsewhere at Dundry and identify the horizon as the highest in the Discites Zone.

3.2.2. Lower Bajocian, Ovale Zone

Faunal horizon Bj-4 is definitely absent here, as at Du-SMR.

Bed 8 a: Faunal horizon Bj-5, *Witchellia romanoides*

The dominant and characteristic faunal element is the eponymous *W. romanoides*, a small species, which is abundant. It marks, with one possible exception, the earliest occurrence in Britain of the genus. It is accompanied by its probable microconchs of the morphogenus *Pelekodites*. Lesser but striking elements are the considerably larger forms of the group of *Witchellia* ['*Zugophorites*' BUCKMAN] *zugophora*, assigned at times in the past to the sonniniid *Euhoploceras* (see the list of faunal horizons above). They may have value for correlation, but not enough material is yet available to characterize range and variability. The type of *W. jugifera* (the Latin version of Greek *zugophora*) came from Swabia but from an unknown horizon. Small otoitids variously assigned to *Emileites* [M] and *Trilobiticeras* or *Otoites* [m], discussed further below, are also prominent but have long ranges. The large *Fissilobiceras* is also striking but is not closely age-diagnostic.

The Bj-5 horizon was originally introduced for the fauna of this bed at Dundry (CALLOMON & CHANDLER 1990) and this appears to continue to be the only locality at which it has so far been recognized in Britain. At Bruton it is absent, almost certainly lost in a stratigraphical non-sequence, and this appears also to be the case in the Sherborne-Bradford Abbas area of northern Dorset.

The type of *W. romanoides* came from the Valleé de Valaury near Toulon in southern France, out of a hard condensed ferruginous bed 0.3–0.7 m thick lying in a sequence of 200 m of poorly fossiliferous but pre-Upper Bathonian limestones. The section was described by ZURCHER (1885: 9–10) and the ammonite fauna from this bed was described by DOUVILLÉ (1885), including *W. romanoides* (some additional details are given by LANQUINE (1929: 227–229) but they add nothing of significance). The fauna of this bed bears a remarkable overall resemblance to that of Bj-5 at Bruton, but does not help in refining the English succession further.

The distinction between Bj-5 and the underlying horizon Bj-4 is clear. Its most striking feature is the total absence in the latter of *Witchellia*. The citation of *W.* aff. *romanoides* in CALLOMON & CHANDLER (1990) was in error. Bj-4 was originally introduced (CALLOMON & CHANDLER 1990) for the 'post-*discites* beds' of BUCKMAN (1910a: 77 and tab. 3) on Waddon Hill, near Beaminster in south Dorset. As its name implies, *Hyperlioceras* is now absent, or at best rare. It also already carries the true *Fissilobiceras ovale* and has therefore been included in the Ovale Zone as its lowest horizon. It also yields *Bradfordia* in some abundance and is named after the species, *B. inclusa* BUCKMAN, of which it is the type horizon and Waddon Hill is the type locality.

The relationship of Bj-5 to its overlying horizons, Bj-6a, b, c, presents some problems that are discussed below.

Bed 8 b: [Faunal horizon 'Bj-6, *Fissilobiceras ovale*' olim]

This bed has yielded the most diverse fauna. The frequency of occurrence varies somewhat within the bed and an attempt was made to separate the collections from different levels within it – parts 8 b(i), 8 b(ii) and 8 b(iii). But no clear lithological breaks could be recognized in a bed that is intensely burrowed. The taphonomy of the smaller specimens suggests that there may have been some mixing in a sediment that remained unconsolidated for a period comparable to that of its accumulation. But the large ammonite discs are flat-lying and undoubtedly in correct relative positions. They make up the most striking element of the fauna, consisting of the distinctive *Fissilobiceras* and another group of large forms of somewhat uncertain affinities, most closely comparable to a common Swabian species tentatively assigned to the genus *Shirbuirnia*, *Sh. gingensis* (WAAGEN). These together were BUCKMAN's "*Sonninia ovalis* (QUENSTEDT)", after which the "*ovalis* Bed" was named. The horizon seemed to be widely recognizable – in the Sherborne area, at Oborne and Sandford Lane, at Bruton and in the Cotswolds – and hence to make a fine marker for correlations.

Subsequently, further faunal horizons at about this level were recognized at Bruton. The section in the railway-cutting through Lusty Hill was first described by RICHARDSON (1916: 495) and reproduced in modified form by DIETZE et al. (2001, fig. 1), the beds having been renumbered in ascending order as is more the convention today. Some new collections were described by PARSONS (1979: 150). The section was intensively resurveyed by two of us (RBC, JHC) in the 1990s (details to be published). The anchor-point in the succession appeared to be bed 5 or the top of the underlying bed 4 (RICHARDSON's bed 6), with large *Fissilobiceras*, resembling the forms known from Dundry, therefore Bj-6. There were no signs of *Witchellia romanoides*, Bj-5, the earliest forms of this genus known at the time, which would have been expected below. But there were instead two further assemblages of Witchelliae in turn not known at Dundry: one below Bj-6, in the main body of bed 4 and one above, bed 6 (RICHARDSON's bed 4). Above that came a fauna resembling that from Dundry labelled Bj-7. So on the assumption that the three assemblages from beds 4, 5, 6 in ascending order lay above Bj-5 but below Bj-7, the original Bj-6 of 1990 had to be replaced by three, Bj-6a, Bj-6b and Bj-6c, with that of the '*ovalis* Bed' of Dundry in the middle, Bj-6b: see fig. 1 in DIETZE et al. (2001). This scheme was introduced in a first revision of the original table of faunal horizons of 1990 in 1995 (CALLOMON 1995: 140, fig. 3) and is reproduced in the emended version of CHANDLER et al. (2006) in Fig. 2 above. To avoid confusion between the use of the same specific name to label an *ovalis* Bed, a faunal *Fissilobiceras ovale* horizon and a standard Ovale Zone, and misconceptions concerning the type horizon of *F. ovale*, which is most probably Bj-4, Bj-6b was renamed the horizon of *Shirbuirnia gingensis*.

The successions of *Witchellia* at Bruton and Dundry are therefore complementary but mutually exclusive. The problem is that the forms of the new assemblage from Bj-6a at Bruton more strongly resemble what have been assumed to be the ancestral stock of the Witchelliinae, namely *Fontannesia* of the Discites Zone, than they do those of Bj-5 at Dundry, *W. romanoides*. Could it be, therefore, that Bj-6a lies in fact below Bj-5? Could it be that the assemblage at Bruton assigned to Bj-6b is then not the same as that assigned to Bj-6b at Dundry and that the whole packet of strata at Bruton assigned to Bj-6a–6c lies below Bj-5? We cannot answer these questions with the new collections from Du-LDW alone.

Upwards, we cannot positively affirm or exclude the presence of some elements of the assemblages of Bj-7a or Bj-7b in Bed 8, for individual morphospecies of the Witchelliinae tend to range over several faunal horizons (see below). None of the ancillary elements of the faunas are yet sufficiently well known to be reliable guidespecies for close time-correlations. The type horizon of the unmistakable *Emileia* (aff.) *dundriensis* shown here on plates 10 and 11 was in fact Bj-8a at Du-SMR. What the rich new collections suggest is that the ranges of some species are longer than had been supposed. There are indications of some faunal differentiation between Beds 8 b(i), b(ii) and b(iii) but they are insufficient to yield any firm conclusions. In summary, therefore, beds 8 b(i)–8 b(iii) cannot at present be assigned to any specific faunal horizons but continue to include what was the original Bj-6.

4. Notes on the ammonite fauna

4.1. Sonniniidae BUCKMAN, 1892

The Sonniniidae of Europe are one of the best documented and longest known groups of Middle Jurassic ammonites. Our knowledge has however been based principally on collections from about three levels well separated in time. The evolutionary changes in morphology that had occurred in the intervals inbetween, together with the wide intraspecific variability that characterises all members of the family, led to a profusion of morphogeneric taxa the phyletic relationships between which were not clear. Two main groups could however be discerned, forming phylogenetic clades with quite separate roots. They were formally separated by CALLOMON & CHANDLER (in CHANDLER et al. 2006), who took out the group of *Witchellia* as the subfamily Witchelliinae (see below). That left the remainder as the subfamily Sonniniinae.

4.1.1. Sonniniinae BUCKMAN, 1892

The subfamily Sonniniinae is clustered around a main phyletic strand leading to the genus *Sonninia* itself. The three levels at which this strand was sampled were roughly as follows.

(a) Main line:

Bj-1–Bj-3, Discites Zone: *Euhoploceras*, *acanthode-modestum* group (revised by SANDOVAL & CHANDLER 2000)

Bj-7–Bj-8, Laeviuscula Zone: *Euhoploceras*, *adicrum* group–*Papilliceras*/*Prepapillites*, *arenatus* group (revised by DIETZE et al. 2005)

Bj-11, Sauzei Zone: *Sonninia* s. s.

As more material came to hand, it became increasingly difficult to draw any systematic boundaries between these groups at generic level and so they were all subsumed into the single phylogenus *Sonninia*, retaining some of the other names as morphosubgenera of *Sonninia* for convenience. The interconnecting transients in the Ovale Zone were very poorly known. The new collections from Dundry serve now to illustrate some of these.

(b) Subsidiary elements: Additional lesser but phyletically separate groups within the Sonniniinae include *Shirbuirnia* BUCKMAN, 1910 (Laeviuscula Zone) (also reviewed in DIETZE et al. 2005), *Pseudoshirbuirnia* DIETZE et al., 2005 and *Sonninites* BUCKMAN, 1923 (top Laeviuscula – Sauzei Zones). There are indications of yet others – see below.

The *Sonninia* fauna of the Ovale Zone of Du-LDW contains typical transients (*S.* aff. *adicra*, Pl. 2, Fig. 1; *S. pseudotrigonata*, Pl. 2, Fig. 2) of the *Euhoploceras* line. Of special interest are specimens such as *S.* aff. *haugi* (Pl. 1, Fig. 1) that represent morphs intermediate between the morphogenera *Euhoploceras* and *Prepapillites*. The inner whorls are "*Euhoploceras*"-like, the bodychamber compressed with a high keel resembling *Prepapillites* but lacking papillae. Most specimens from Du-LDW are microconchs or juveniles. The corresponding [M] may be found in morphs centred on "*Papilliceras*" *pseudoarenatum* MAUBEUGE (1951) or "*Sonninia*" *luciusi* MAUBEUGE (1951).

Specimens resembling '*Dundryites*' *albidus* BUCKMAN (1926, TA 6, pl. 687) are fairly common in bed 8 b (Pl. 3) and range upwards into the Laeviuscula Zone. The holotype came from BUCKMAN & WILSON's section I, bed 6, 'Western End, near Castle Farm' (see § 2 above), the equivalent of our bed 8 b(i). Smaller specimens (topotype, Pl. 3, Fig. 2) show a strong resemblance to *Witchellia* (cf. Pl. 4, Fig. 3a) in their coiling, flat-sided whorl-section and steep, sharp-edged umbilical walls. The keels are however set on a rounded to fastigate venter rather than the subquadrate venter, tending to bisulcate, typical of *Witchellia* (cf. Pl. 4, Fig. 3b). The most striking difference however lies in the relatively complex septal sutures (Pl. 3, Fig. 1), seen equally clearly in BUCKMAN's type, differing from the more simplified sutures typical of the Witchelliinae and resembling more closely those of the Sonniniinae. For this reason we exclude the taxon from the Witchelliinae and revive BUCKMAN's genus *Dundryites*. *D. albidus* is then possibly the ancestor of *Sonninites* (type species *S.* **felix*) in the Sauzei Zone.

4.1.2. Witchelliinae CALLOMON & CHANDLER, 2006

These range through bed 8 (see lists above) but dominate in the lower part, bed 8 a. The variability of the forms at any one level can be wide so that morphospecies based on individual morphs, of which the literature carries many, can have long vertical ranges. In many cases the precise horizon of the types is not known. Conversely, individual morphospecies can make poor age-diagnostic guide-fossils. Exceptions occur when material is abundant and the variability can be mapped. In such cases the general conclusion that all the morphs of a genus occurring together are merely intergrading variants of a single biospecies is reconfirmed (see CHANDLER et al. 2006).

One such case here is that of bed 8 a, the horizon of the *Witchellia romanoides* assemblage, the type horizon of the original English faunal horizon Bj-5. The variability of this assemblage is in fact rather low. The typical size is relatively small (Pl. 4, Figs. 1, 3, 4), the whorl-section compressed with flat sides and sharp umbilical edge, the keel subdued and bordered by narrow flat margins or even sulci, the ribbing faint or subdued, lacking tubercles or spines. Another typical specimen was figured by PARSONS (1979, pl. 1, figs. 3, 5) from the same level at nearby Barns Batch. The species *Ludwigia romanoides* DOUVILLÉ was based on two syntypes (1885, pl. 3, figs. 3, 4) and came from a condensed bed at a locality in SE France (see above, § 3, bed 8 a). We refigure casts of them here photographically for the first time (Pl. 4, Figs. 2, 5) and designate DOUVILLÉ's syntype I (pl. 3, fig. 4, here Pl. 4, Fig. 2) to be the lectotype.

A somewhat larger, more strongly-ribbed variant is shown here on Pl. 6, Fig. 2 as *W.* cf. *sayni*. It is transitional to forms one of which, from the same locality as *L. romanoides*, was also figured by DOUVILLÉ (1885, pl. 2, fig. 1), as *Ludwigia corrugata*. This in turn became, together with the other four specimens on DOUVILLÉ's pl. 2, a syntype of *Witchellia sayni* HAUG, 1893 (HAUG 1893: 308). A cast of this specimen

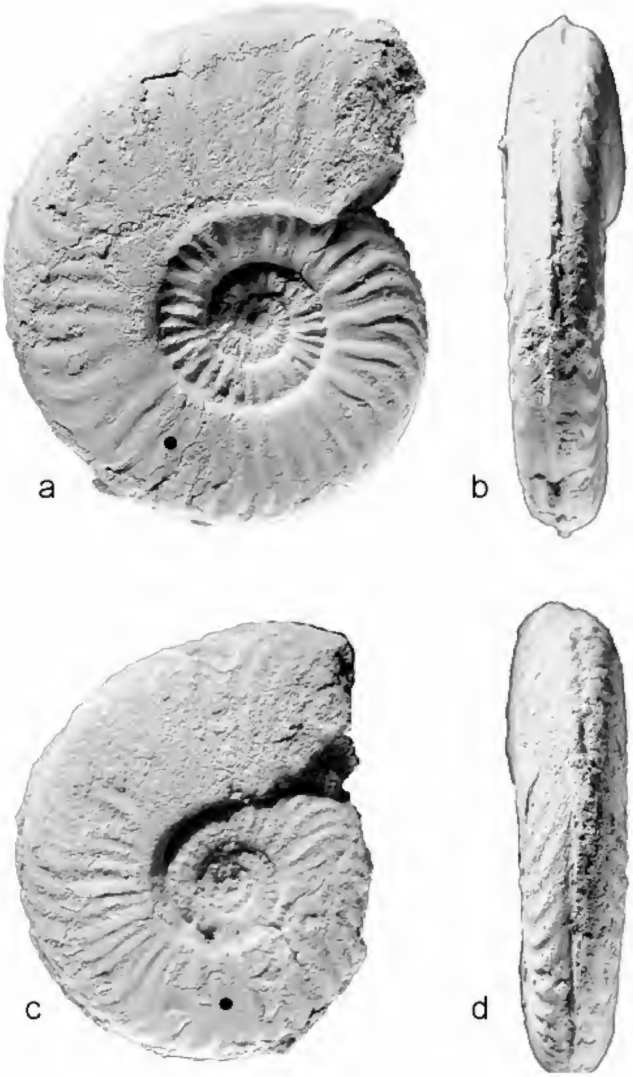

Fig. 3. *Witchellia connata* (Buckman) [M]. **a–b**: nearly complete adult; bed 8, loose; SM X40300. **c–d**: nearly complete adult; bed 8 b(ii); SM X40301. – All figures natural size. Black spots on lateral views indicate the beginning of the bodychamber at the last septum.

is also figured here on Pl. 6, Fig. 1 and designated lectotype of the species *sayni*. Yet larger but also closely related forms are represented by *Witchellia jugifera* (Waagen, 1867). A cast of the lectotype (designated by Dietze et al. 2005: 60), from Gingen in Swabia, is also figured here on Pl. 5, Fig. 3. Closely related to this species is then the equally large *W. ('Zugophorites') zugophora* Buckman (1922, TA 4, pl. 341). This came from Leckhampton in the Cotswolds, from the Gryphite Grit, a bed whose precise age could not be determined more closely than Ovale Zone (Parsons 1980).

Going upwards, the variability of the forms we assign to *Witchellia* in beds 8 b becomes higher. Besides typical *W. romanoides*, which persists, there occur many of the other morphospecies that have been described in the past from the Ovale and Laeviuscula Zones of southern England. The distributions over the range of variability do however change with time, from the rather smooth forms of Bj-5 to increasingly more strongly ribbed ones. One of these is shown on Pl. 6, Fig. 3, which, although still of similar size to *W. romanoides*, matches precisely the inner whorls of the type of *W. zugophora*. Two others (Fig. 3) closely match the type of *W. ('Zugella') connata* (Buckman) (1927, TA 7, pl. 750), whose origin is however also uncertain. A specimen of intermediate size (Pl. 7, Fig. 2) resembles wholly septate *W. ('Dundryites') pavimentaria* (Buckman) (1927, TA 7, pl. 751) and another large one on Pl. 7, Fig. 1 resembles *W. patefactor* Buckman (1923, TA 4, pl. 410), from the upper Laeviuscula Zone, Bj-10. An involute, smooth morph is figured on Pl. 5, Fig. 1 as *W.* cf. *rubra*. One feature that does seem to persist throughout the whole range of *Witchellia*, and is now confirmed at the lower end of the range, is the occurrence together at all levels of small and large forms, undoubtedly macroconchs, differing essentially only in adult sizes, by factor of two or more: *W. romanoides* – *jugifera* in Bj-5, *W. spinifera* – *platymorpha* in Bj-10. It raises the suggestion of possible ontogenetic polymorphism as cause. Similar observations can be made in other, not closely related groups of Middle Jurassic ammonites (see below in the Otoitidae).

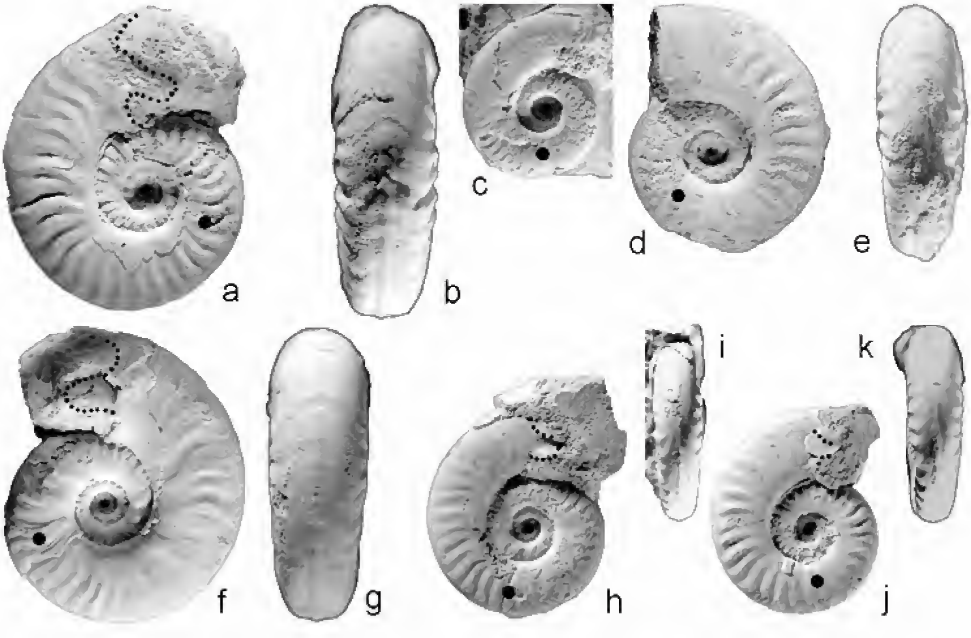

Fig. 4. a–b, d–g: *Pelekodites pelekus* Buckman [m]. **a–b**: complete adult with base of the lappet, matching exactly the holotype from Dundry (Buckman 1923, TA 4, pl. 399); bed 8 b(ii); SM X40302. **d–e**: bed 8 a; SM X40303. **f–g**: bed 8 b(i); SM X40304. – **c**: *Pelekodites* aff. *minimus* (Hiltermann) [m]; bed 8 b(ii); SM X40307. – **h–k**: *Pelekodites* cf. *aurifer* (Buckman) [m], complete adults with lappets. **h–i**: bed 8 b(i); SM X40305. **j–k**: bed 8 a; SM X40306. – All figures natural size. Black spots on lateral views indicate the beginning of the bodychamber at the last septum.

The presumed microconchs of *Witchellia* are also abundant (Fig. 4). Three monotypic nominal genera were based on type-species from Dundry: *Pelekodites *pelekus* BUCKMAN, 1923, *Spatulites *spatians* BUCKMAN, 1928 and *Maceratites *aurifer* BUCKMAN, 1928. Of these, two could be closely matched with specimens in the new collections: *P. pelekus* (Figs. 4a–b, d–g, beds 8 a, 8 b(i) and 8 b(ii)) and *P.* cf. *aurifer* (Figs. 4h–k, beds 8 a–8 b(i)). The types of these came however from higher levels. A small specimen (Fig. 4c) may be compared with *'Sonninia' minima* HILTERMANN (1939: 174, pl. 12, figs. 4, 6). The original descriptions were not precise, but re-examination of the specimens shows the matrix to be more ferruginous, with larger brown ooliths, than anything in bed 8, pointing to levels in the 'Upper White Ironshot', Laeviuscula Zone, well above the Ovale Zone. (The type of *Sp. spatians* came unambiguously from Bj-10a or Bj-10b. Another very similar lappeted microconch is *Nannoceras *nannomorphum* BUCKMAN (1923, TA 5, pl. 445), from the Discites Zone, supporting the suggested root of the dimorphic lineage of *Witchellia* in the genus *Fontannesia* BUCKMAN, 1902).

4.2. Hammatoceratidae BUCKMAN, 1887

Fissilobiceras is one of the most common ammonites from bed 8 a up to bed 8 b(ii) (Pl. 8). The genus has been recently reviewed in detail by DIETZE et al. (2005). Most of the specimens belong to the morphospecies *F. ovale* (QUENSTEDT), which when complete can reach sizes up to 0.5 m.

The ammonites from bed 8 figured by CALLOMON & CHANDLER (1990, pl. 1, fig.1; pl. 2, fig. 1) as *Sonninia ovalis* are more evolute than the typical forms of *Fissilobiceras*, whose intraspecific variability in this character is otherwise low. Their systematic position remains somewhat uncertain. The suture-line of the smaller of the two, a wholly septate nucleus (pl. 2, fig. 1) does have a typically fissilobate complexity but that of the larger one (pl. 1, fig. 1) is less so, more like that of a sonniniid. It was therefore tentatively assigned to the sonniniid genus *Shirbuirnia*: cf. *Sh. gingensis* (WAAGEN) trans α (DIETZE et al. 2005, fig. 23), from the Ovale Zone of Donzdorf in the eastern Swabian Alb (see map in DIETZE et al. 2005, fig. 1). Its name was then used to re-label the horizon Bj-6b (CHANDLER et al. 2006, see Fig. 2 here) for the reasons given above (§ 3.2.2.).

4.3. Strigoceratidae BUCKMAN, 1924

The genus *Strigoceras* [M] and its microconchiate counterpart *Cadomoceras* [m] are in course of revision (SCHWEIGERT et al., in preparation) so comments here will be brief. The strigoceratids appear first in the Upper Aalenian. They are fairly common in the beds under investigation (Fig. 5), showing a variability between almost smooth and coarsely ribbed forms, the ribbing ranging from regular to irregular. Here again, a variety of morphospecies has been defined in the past.

The oldest of the appropriate names appears to be one introduced by ETHERIDGE in WRIGHT (1860: 24) in a faunal list of ammonites found at Dundry: *Amm. truellei* (var. *compressus*) D'ORB. There was no description, so even regarding *compressus* as an available name (which it is not, preoccupied), it is a nomen nudum. It was revived by BUCKMAN (in BUCKMAN & WILSON 1896: 701) as *Strigoceras compressum* (ETHERIDGE), with sufficient description to make the name now available: *Str. compressum* (ETHERIDGE MS) BUCKMAN, 1896. A specimen from the 'West End, Castle Farm'

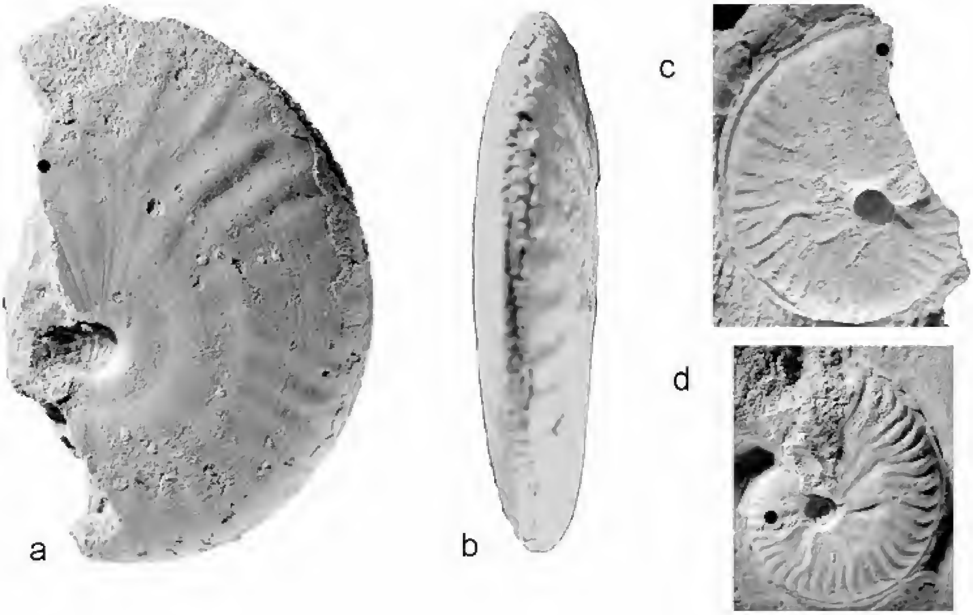

Fig. 5. **a–b**: *Strigoceras strigifer* (Buckman) [M], phragmocone; bed 8 b(ii); SM X40309. – **c–d**: *Strigoceras compressum* Buckman. **c**: complete phragmocone, probably a juvenile; Bed 8 b(ii); SM X40310. **d**: small specimen with some bodychamber, probably also juvenile; Bed 8 a; SM X40311. – All figures natural size. Black spots on lateral views indicate the beginning of the bodychamber at the last septum.

section out of what is clearly our bed 8 a was finally figured by Buckman in 1924 (TA 5, pl. 468) as a 'topotype' (and under yet another new generic name, *Varistrigites*). It was in J. W. Tutcher's collection and is now in the Natural History Museum, London (C.41727). It could not have been in the type series of whatever Buckman had at his disposal in 1896, even if this included whatever Etheridge had collected and named. It would now be almost impossible to retrace this type series. Yet the figured topotype is a fine example of an eminently recognizable species and to conserve this we propose to designate Buckman's topotype of 1924 as neotype, Ovale Zone, horizon Bj-5. New specimens of strigoceratids from the Ovale Zone of Dundry are shown in Fig. 5.

4.4. Otoitidae Mascke, 1907

A revision on the Otoitidae from the Inferior Oolite of southern England is in progress so only a brief treatment will be given here.

Typical ammonites of the genus *Emileia* s. s. and *Otoites* occur in the Ovale Zone of Dundry Hill. The large and evolute specimen shown on Pl. 10, Fig. 1 (Pl. 11, Fig. 2) is close to paratype 3 of *E. dundriensis* (Callomon & Chandler, 2006), while the phragmocone on Pl. 11, Fig. 1 resembles paratype 2. The lower range of typical *Emileia* s. s. and its phyletic roots remain largely unknown but the new discoveries take the genus down into at least the upper Ovale Zone. Small, coarsely-ribbed but otherwise typical *Otoites* occur in bed 8 b(i). They include a form closely resembling *Otoites tumulosus* Westermann (1956, pl. 10, fig. 3). The holotype of this species came from Dundry Hill, but not from the Ovale Bed. Its matrix is that of the Laeviuscula or Sauzei Zone (C. Parsons, pers. comm. V. D. 2006). The coarsely-ribbed and small form (Pl. 10, Fig. 2) has already been well described as *O. douvillei* by Parsons (1977) and shows that the Ovale Zone is at a critical point in the evolution of the dimorphic pair *Emileia*/*Otoites*.

The interpretation of the type species of *Emileites*, *Em. malenotatus* Buckman (1927, TA 6, pl. 702) has long been uncertain because of a poor figure of an imperfect type specimen. Its precise origin appears also to be in some doubt, although Buckman, in the legend to his plate, surmises it to have been the Lower White Ironshot of Dundry. In this he was followed by Parsons (1979). Investigation shows that this ammonite is totally septate at its maximum diameter of 42 mm and that it has the beginning of a planulate stage. Part of the phragmocone and the entire bodychamber are missing. We now have an almost exact match in an incomplete adult specimen from bed 8 b(ii) that carries at least a part of the body chamber (Pl. 9, Fig. 1). Assuming a bodychamber of three-quarters of a whorl, the maximum size would have been some 90 mm. Another complete phragmocone from the same level is shown in Pl. 9, Fig. 2. These ammonites show features typical of *Emileia* s. s.: coronate inner whorls with depressed whorl section later becoming semi-circular and more planulate. The primary ribbing shows long ribs that fade on the bodychamber towards the mouth border. Later members of this group are *E. catamorpha* Buckman in the Laeviuscula Zone and *E. multifida* Buckman and *E. polymera* sensu Rioult in the Sauzei Zone. We therefore treat this group at present as a subgenus of *Emileia*, running in parallel with it into the Sauzei Zone. This would be another example in which a possible explanation for the size differences may lie in ontogenetic polymorphism. It is seen already in *Docidoceras* of the Discites Zone. The subgenus *Emileites* in this sense is most commonly found around Bj-8.

The bulk of the otoitid ammonites found in the Ovale Zone of Dundry Hill (Pl. 9, Figs. 3–5) are smaller and have a development of the shell similar to that seen in the inner and middle parts of the phragmocone of *Emileites malenotatus*. The specimens reach a maximum diameter of only about 40 mm, at which diameter the true *Em. malenotatus* is still septate. But they differ from *Em. malenotatus* in never loosing their coronate whorl-section. The primary ribbing persists to the end of the bodychamber and is most prominent low on the whorl-side, on the umbilical slope. The general character of this group is *Pseudotoites*- or *Frogdenites*-like. Parsons (1977) already recognized that this small-sized, coronate group and the group of *Emileia* proper represent two different clades within the Otoitidae, but he did not state that the type specimen of *Emileites malenotatus* belongs to the "*Emileia*-clade". So neither the generic name *Emileites* nor the specific name *malenotatus* are available for members of this small-sized, cadiconic group, but this is a matter to be considered elsewhere. An available specific name is "*Docidoceras*" *liebi* Maubeuge. For the moment we identify our Dundry specimens as "*Emileites*" [gen. nov.] *liebi* (Pl. 9, Figs. 3–5). As also already pointed out by Parsons, the [m] of this group is the coronate taxon "*Trilobiticeras*" *cricki* Parsons (Pl. 9, Figs. 6–8).

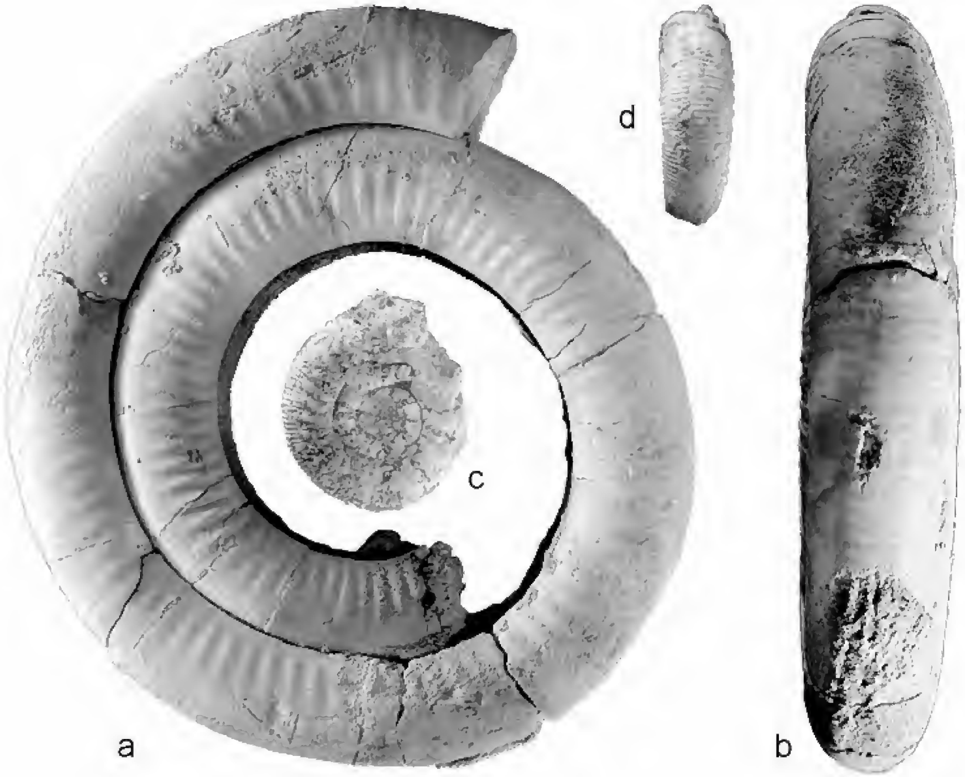

Fig. 6. *Stephanoceras* aff. *richardsoni* (Dietze et al.) [sp. nov.] [M]; bed 8 b(ii); SM X40312. **a–b**: nearly complete bodychamber of 1.6 whorl, maximum diameter 200 mm. **c–d**: nucleus of the same specimen in position as found. – Reduced × 0.5. Black spot on lateral view indicates the beginning of the bodychamber at the last septum.

4.5. Stephanoceratidae Neumayr, 1875

The upper part of bed 8 has yielded a specimen of a *Stephanoceras* unlike any other so far found in Britain (Fig. 6: *St.* aff. *richardsoni* (Dietze et al., 2001)). The earliest *Stephanoceras* proper known there occurs in the Aalenian, Concavum Zone (Callomon & Chandler 1990, pl. 3, fig. 1, Aa-12/13; pl. 2, fig. 2, Aa-14/15). Specimens from the Lower Bajocian, Discites Zone, Bj-1, -2, include *St. ['Docidoceras'] perfectum* Buckman (1922, TA 4, pl. 314) (and see Chandler & Sole 1996). Then there was a gap until the boundary Ovale/Laeviuscula Zone, Bj-7a, with *St. richardsoni*. Occasional specimens have also been found higher in the Laeviuscula Zone, but the genus becomes abundant only in the Sauzei Zone (Bj-11a) and thence upwards into the Humphriesianum Zone.

The new specimen resembles *St. richardsoni* (and its closely related *St. brutonense* (Dietze et al., 2001)) in its highly evolute and densely ribbed bodychamber, but differs from them in the inner whorls, which are more involute and coarsely ribbed in *St. richardsoni*. The nearest comparisons are with material from elsewhere in Europe. Similar bodychambers are found in the 'early stephanoceratids' of the Tethyan Province, *St. ['Coeloceras'] longalvum* (Vacek) from San Vigilio in northern Italy (lectotype refigured in WESTERMANN 1964, pl. 6, fig. 1, age uncertain, possibly Lower Bajocian but probably Middle Aalenian (CALLOMON et al. 1995), and type species of a new genus *Riccardiceras* WESTERMANN, 1995) or *St. telegdirothi* (GECZY) from Hungary (redescribed with stratigraphy by CRESTA & GALACZ 1990). Similar forms are cited as common at Cap Mondego in Portugal (FERNÁNDEZ-LÓPEZ et al. 1988) and one of these from the Ovale Zone figured by ROCHA et al. (1990, pl. 3, fig. 5) is particularly close. But the closest match with the Dundry specimen seems to be with the '*Riccardiceras*' cf. *richardsoni* figured by DIETZE et al. (2001, fig. 5) from the Ovale Zone of the Scheffheu, near Blumberg in southwestern Germany. The rarity of stephanoceratids in the Aalenian and Lower Bajocian of southern Britain and Germany is a reflection of their bioprovincialism.

4.6. Oppeliidae DOUVILLÉ, 1890

The conventional family Oppeliidae contains two clearly distinguishable phyletic strands from its early stages: the Oppeliinae proper and the Bradfordiinae CALLOMON, 1981 (p. 143). Of these, the Bradfordiinae can be traced back in England to

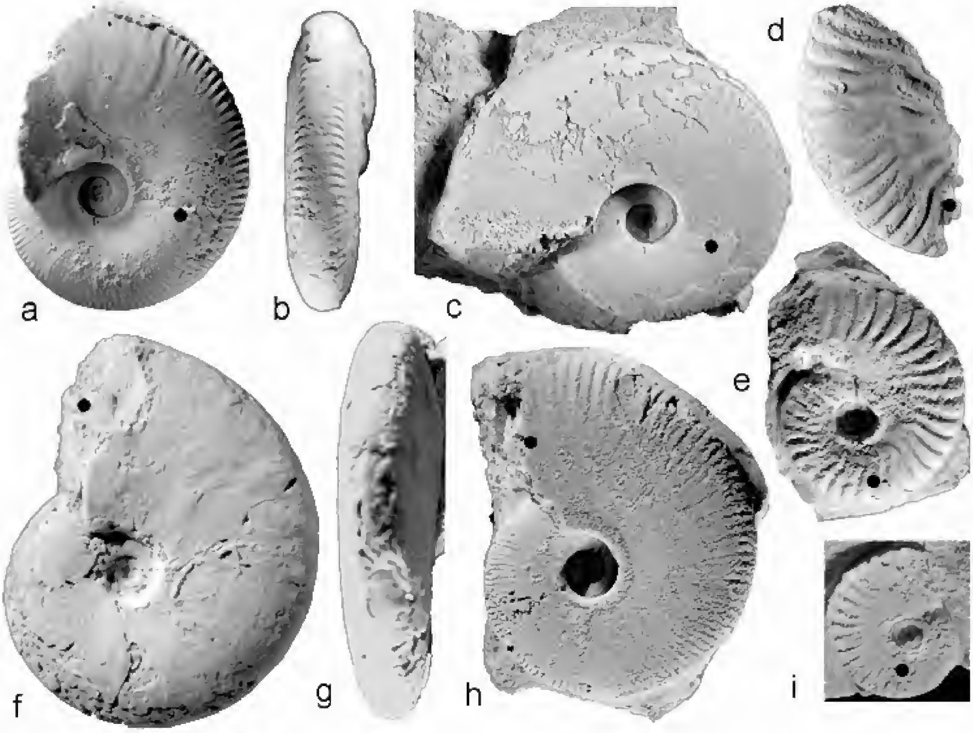

Fig. 7. **a–b**: *Bradfordia* cf. *praeradiata* (DOUVILLÉ) [M]; bed 8 b(ii); SM X40313. – **c**: *Lissoceras*? cf. *semicostulatum* BUCKMAN; bed 8 b(i); SM X40315. – **d–e, i**: *Hebetoxyites hebes* BUCKMAN, topotypes. **d**: bodychamber fragment; bed 8 b(ii); SM X40317. **e**: small specimen, [?m]; bed 8, loose; SM X40318. **i**: juvenile?; bed 8 b(ii); SM X40319. – **f–g**: *Oppelia*? sp. [M]; bed 8 a; SM X40316. – **h**: *Bradfordia* cf. *costidensa* IMLAY [M]; bed 8 b(ii); SM X40314. – All figures natural size. Black spots on lateral views indicate the beginning of the bodychamber at the last septum.

Bradfordia costata BUCKMAN, 1910 in the Concavum Zone (Aa-15) of the Upper Aalenian (CHANDLER & SOLE 1996) and then traced upwards relatively unchanged into the Sauzei Zone. The most striking and conservative features are a broad, smooth, spiral depression low on the whorl-side at the raised sharp edge of a steep to overhanging umbilical wall, secondary ribbing confined to and persisting on the latero-ventral shoulder high on the whorl-side, and smooth rounded venters. Typical forms are relatively common at Dundry (Fig. 7a–b, h) and another typical form was described by DOUVILLÉ from Toulon as *Oppelia praeradiata* (1885, pl. 3, fig. 7, non fig. 6, the lectotype, of unknown age, from Normandy). The forms illustrated here (Fig. 7) from Dundry are more densely and finely ribbed than *B. praeradiata* and *B. costata* described by BUCKMAN (1910b). The most fine-ribbed of them, Fig. 7h, is most closely matched by a species from Alaska described by IMLAY (1964), *B. costidensa*, from the Talkeetna Mountains.

The second clearly-defined strand is based on *Oppelia* itself, going back to the type species *O. subradiata* (SOWERBY) at the base of the Humphriesianum Zone. Then there are various other genera known over only short ranges that seem to fall somewhere in between, including *Amblyoxyites* BUCKMAN, *Toxamblyites* BUCKMAN, *Stegoxyites* BUCKMAN and perhaps *Hebetoxyites* BUCKMAN. But the leading question relates to the relationship between the Bradfordiinae and Oppeliinae themselves. It has long been assumed that the latter developed from the former, but where and when has remained mysterious. The earliest occurrence of anything resembling *Oppelia* is therefore of great interest. One candidate is *Praeoppelia gracilobata* (VACEK) from the Middle Aalenian, Bradfordensis Zone of San Vigilio (CALLOMON et al. 1995). We have now a specimen (Fig. 7f–g) from bed 8 a that also seems closer to *Oppelia* than it does to *Bradfordia*, taking the range down from Bj-13 to Bj-5. Another specimen in this group (Fig. 7c) bears some resemblance to *Lissoceras semicostulatum* BUCKMAN (1923, TA 4, pl. 400), from the Laeviuscula Zone at about Bj-8, a genus also of cryptogenic origin then ranging up almost unchanged into the Cretaceous.

Finally, *Hebetoxyites *hebes* BUCKMAN (1924, TA 5, pl. 475), whose type also came from the 'Lower Ironshot' of Dundry, probably also from the West End quarry (teste BUCKMAN), at a level equivalent to our 8 b(ii). Specimens of this species are rare at Dundry and we have found it only in the higher part of bed 8 (Fig. 7d, e, i, topotypes). *Hebetoxyites* lacks strigations and a hollow floored keel, characteristic of strigoceratids. On these grounds we exclude it from the Strigoceratidae (FERNÁNDEZ-LÓPEZ 1985) and leave it in the Oppeliidae s. l. for the present.

5. Conclusions

The new excavation at Dundry, Little Down Wood, was aimed at providing a more detailed look at a part of the Inferior Oolite that has been poorly documented in the past. It lies in the Ovale Zone of the Lower Bajocian Stage, in beds that have been widely lost through intra-formational erosion in Dorset or, where developed in expanded sequences in the Cotswolds, in beds that are almost devoid of the critical time-diagnostic guide-fossils, the ammonites. At Dundry the Ovale Zone is in part represented by a single bed, bed 8, that is very rich in ammonites. In terms of the biostratigraphical classification adopted today for most of the Inferior Oolite of

England, it forms the type succession for two of the original ammonite faunal horizons introduced in 1990, that of Bj-5, *Witchellia romanoides* in the lower part and that of Bj-6, *Fissilobiceras ovale* in the upper part of the bed. There were reasons to believe that the latter might, with very precise collecting, be further divisible. The bed was therefore opened and a large collection of ammonites made from it.

The fauna of Bj-5 was amply represented but yielded nothing stratigraphically very new. It did however strengthen the correlation with two almost equally precise horizons abroad, in the Ovale Zone of Swabia and in an area near Toulon in southern France. Similarly, despite best efforts and the recovery of a large collection, attempts to recognize further biostratigraphical subdivisions in Bj-6 were unsuccessful. What has however been achieved is the amplification of the taxonomy of many of the ammonite groups, previously known only from scattered records. These include genera of great interest in the framework of the evolution of the ammonites as a whole, especially in times in the Bajocian that saw a great world-wide diversification of these molluscs. An incoherent complexity of morphogenera and morphospecies is being condensed into a much simpler, more natural, phylogenetic classification, especially in the Bajocian. To this end, the new collections are of great significance. Their fuller evaluation will take time.

6. References

BUCKMAN, S. S. (1887): A monograph of the ammonites of the Inferior Oolite Series. Pt (i), 1–24; London (Palaeontographical Society).

BUCKMAN, S. S. (1893): The Bajocian of the Sherborne district: its relation to subjacent and superjacent strata. – The Quarterly Journal of the Geological Society of London, **49**: 479–522.

BUCKMAN, S. S. (1910a): Certain Jurassic (Lias-Oolite) strata of South Dorset, and their correlation. – The Quarterly Journal of the Geological Society of London, **66**: 52–89.

BUCKMAN, S. S. (1910b): Certain Jurassic ('Inferior Oolite') species of ammonites and brachiopoda. – The Quarterly Journal of the Geological Society of London, **66**: 90–108.

BUCKMAN, S. S. (1909–1930): Yorkshire Type ammonites/Type Ammonites, **1–7**, 790 pls.; London (Wheldon & Wesley).

BUCKMAN, S. S. & WILSON, E. (1896): Dundry Hill: its upper portion, or the beds marked as Inferior Oolite (g 5) in the Maps of the Geological Survey. – The Quarterly Journal of the Geological Society of London, **52**: 669–720.

CALLOMON, J. H. (1981): Superfamily Haplocerataceae. – In: DONOVAN, D. T., CALLOMON, J. H. & HOWARTH, M. K.: Classification of the Jurassic Ammonitina. – In: HOUSE, M. R. & SENIOR, J. R. (eds.): The Ammonoidea. – Systematics Association Special Volume, **18**: 101–155; London etc. (Academic Press).

CALLOMON, J. H. (1995): Time from fossils: S. S. BUCKMAN and Jurassic high-resolution geochronology. – In: LE BAS, M. J. (ed.): Milestones in Geology. – Geological Society, London, Memoir, **16**: 127–150.

CALLOMON, J. H. & CHANDLER, R. B. (1990): A review of the ammonite horizons of the Aalenian–Lower Bajocian Stages in the Middle Jurassic of Southern England. – Memorie descrittive della carta geologica d'Italia, **40**: 85–111.

CALLOMON, J. H. & CHANDLER, R. B. (2006): Notes on the ammonite faunas. – In: CHANDLER, R. B., CALLOMON, J. H., KING, A., JEFFREYS, K., VARAH, M. & BENTLEY, A.: The stratigraphy of the Inferior Oolite at South Main Road Quarry, Dundry, Somerset. – Proceedings of the Geologists' Association, **117**: 365–372.

CALLOMON, J. H., CRESTA, S. & PAVIA, G. (1995): A revision of the classical Aalenian succession in the Middle Jurassic of San Vigilio, Lake Garda, northern Italy. – Géobios, Mémoir spécial, **17**: 103–110.

Chandler, R. B., Callomon, J. H., King, A., Jeffreys, K., Varah, M. & Bentley, A. (2006): The stratigraphy of the Inferior Oolite at South Main Road Quarry, Dundry, Somerset. – Proceedings of the Geologists' Association, **117**: 345–375.

Chandler, R. B. & Sole, D. T. C. (1996): The Inferior Oolite at East Hill Quarry, Bradford Abbas, Dorset. – Proceedings of the Dorset Natural History and Archaeological Society, **117**: 103–108.

Cresta, S. & Galacz, A. (1990): Mediterranean basal Bajocian ammonite faunas. Examples from Hungary and Italy. – Memorie descrittive della carta geologica d'Italia, **40**: 165–198.

Davies, A. M. (1930): Editorial note. – In: Buckman, S. S.: Type Ammonites, **7**: 16–79.

Dietze, V., Chandler, R. B., Schweigert, G. & Auer, W. (2001): New Stephanoceratids (Ammonitina) from the Lower Bajocian of Bruton (Somerset, S England) and Achdorf (Wutach area, SW Germany). – Stuttgarter Beiträge zur Naturkunde, Serie B, **312**: 21 pp.

Dietze, V., Callomon, J. H., Schweigert, G. & Chandler, R. B. (2005): The ammonite fauna and biostratigraphy of the Lower Bajocian (Ovale and Laeviuscula Zone) of E Swabia (S Germany). – Stuttgarter Beiträge zur Naturkunde, Serie B, **353**: 82 pp.

Douvillé, H. (1885): Sur quelques fossiles de la zone à *Ammonites sowerbyi* des environs de Toulon. – Bulletin de la Société Géologique de France, (3) **13**: 12–44.

Douvillé, H. (1890): Sur la classification des Cératites de la Craie. – Bulletin de la Société Géologique de France, (3) **18**: 275–292.

Fernández-López, S. (1985): El Bajociense en la Cordillera Ibérica. 848+23 pp.; Madrid (Facultad de Ciencias Geológicas, Depart. de Paleontologia, Universidad Complutense).

Fernández-López, S., Henriques, M. H., Mouterde, R., Rocha, R. B. & Sadki, D. (1988): Le Bajocien inferieur du Cap Mondego (Portugal) – essai de biozonation. – In: Rocha, R. B. & Soares, A. F. (eds.): 2nd Int. Symposium on Jurassic Stratrigraphy: 301–333; Lisboa.

Haug, É. (1893): Étude sur les ammonites des étages moyens du système Jurassique. – Bulletin de la Société Géologique de France, (3) **20**: 277–333.

Hiltermann, H. (1939): Stratigraphie und Paläontologie der Sonninienschichten von Osnabrück und Bielefeld. – Palaeontographica, Abteilung A, **90**: 109–209.

Imlay, R. W. (1964): Middle Bajocian ammonites from the Cook Inlet region, Alaska. – U.S. Geological Survey Professional Paper, **418-B**: 1–61.

Lanquine, A. (1929): Le Lias et le Jurassique des Chaînes Provencales. I. Le Lias et le Jurassique inférieur. – Services de la Carte Géologique de la France et des Topographies Souterraines, **32**, no. 173: 385 pp.

Maubeuge, P. L. (1951): Les ammonites du Bajocien de la région frontière Franco-Belge. – Mémoires de l'Institut royal des Sciences naturelles de Belgique, (2) **42**: 104 pp.

Parsons, C. F. (1974): The *sauzei* and «so called» *sowerbyi* zones of the Lower Bajocian. – Newsletters on Stratigraphy, **3**: 153–180.

Parsons, C. F. (1977): Two new Bajocian microconch otoitid ammonites and their siginificance. – Palaeontology, **20**/1: 101–118.

Parsons, C. F. (1979): A stratigraphic revison of the Inferior Oolite of Dundry Hill, Bristol. – Proceedings of the Geologists' Association, **90**/3: 133–151.

Parsons, C. F. (1980): Aalenian and Bajocian correlation chart. – In: Cope, J. C. W. (ed.): A correlation of Jurassic rocks in the British Isles. Part two: Middle and Upper Jurassic. – Geological Society, London, Special Report, **15**: 3–21.

Richardson, L. (1916): The Inferior Oolite and contiguous deposits of the Doulting-Milborne Port district (Somerset). – The Quarterly Journal of the Geological Society of London, **71**: 473–520.

Rocha, R. B., Henriques, M. H., Soares, A. F., Mouterde, R., Caloo, B., Ruget, C. & Fernández-López, S. (1990): The Cabo Mondego section as a possible Bajocian boundary stratotype. – Memorie descrittive della carta geologica d'Italia, **40**: 49–60.

Sandoval, J. & Chandler, R. B. (2000): The sonniniid ammonite *Euhoploceras* from the Middle Jurassic of south-west England and southern Spain. – Palaeontology, **43**: 495–532.

Vacek, M. (1886): Über die Fauna der Oolithe von Cap San Vigilio, verbunden mit einer Studie über die obere Liasgrenze. – Abhandlungen der kaiserlich-königlichen Geologischen Reichsanstalt, **12**: 57–105.

WAAGEN, W. (1867): Über die Zone des *Ammonites sowerbyi.* – Benecke's Geognostisch-paläontologische Beiträge, **1**: 507–668.
WESTERMANN, G. E. G. (1956): Monographie der Otoitidae (Ammonoidea). – Beihefte zum Geologischen Jahrbuch, **15**: 364 pp.
WESTERMANN, G. E. G. (1964): Sexual-Dimorphismus bei Ammonoideen und seine Bedeutung für die Taxionomie der Otoitidae. – Palaeontographica, Abteilung A, **124**: 33–73.
WESTERMANN, G. E. G. (1995): Mid-Jurassic Ammonitina from the Central Ranges of Irian Jaya and the origin of the stephanoceratids. – Hantkeniana, **1**: 105–118.
WRIGHT, T. (1860): On the subdivisions of the Inferior Oolite in the south of England, compared with the equivalent beds of that formation on the Yorkshire coast. – Quarterly Journal of the Geological Society, **16**: 1–48.
ZURCHER, M. (1885): Note sur la zone à *Ammonites Sowerbyi* dans le S. O. du département du Var. – Bulletin de la Société Géologique de France, (3) **13**: 9–11.

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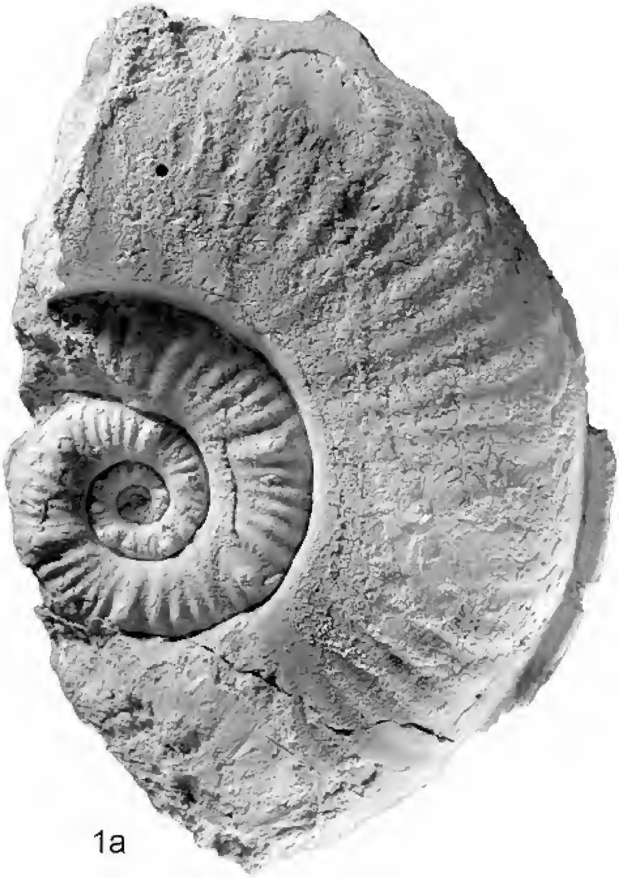
Plate 1

Fig. 1. *Sonninia* aff. *haugi* GILLET [sp. nov.?]. This species seems to be intermediate between the morphogenera *Euhoploceras* and *Prepapillites/Papilliceras*. Bed 8 b(i); SM X40320.

Fig. 2. *Sonninia* cf. *subdecorata* BUCKMAN [m]. Adult, the last sutures approximated. Bed 8 a; SM X40321.

Fig. 3. *Sonninia* cf. *subdecorata* BUCKMAN [m]. Another adult but wholly septate, probably large [m]. Bed 8 a; SM X40322.

All figures natural size. Black spots on lateral views indicate the beginning of the bodychamber at the last septum.



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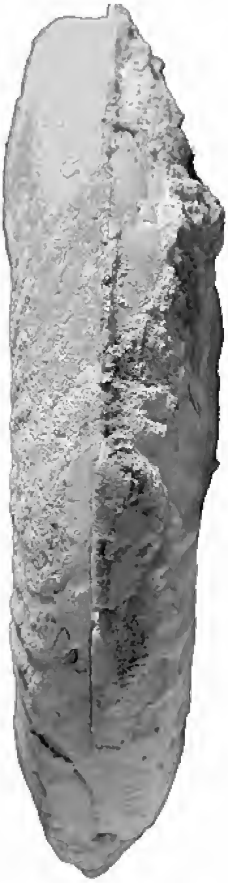

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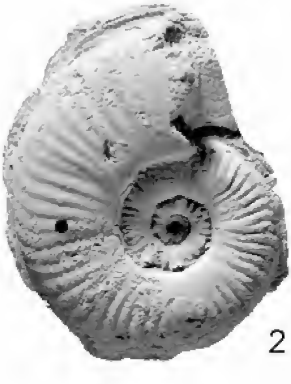

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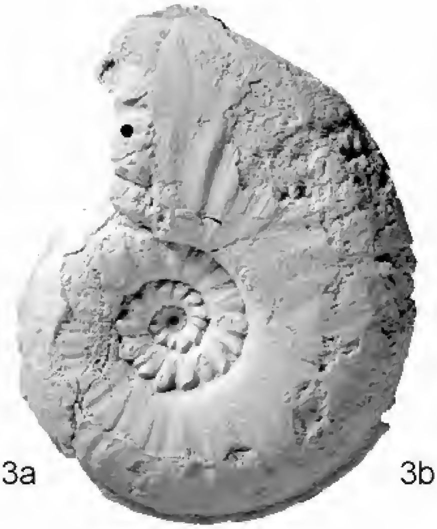

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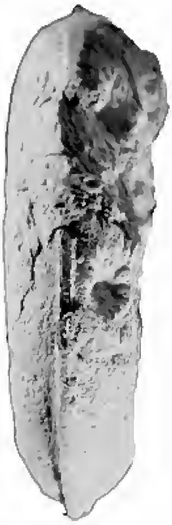


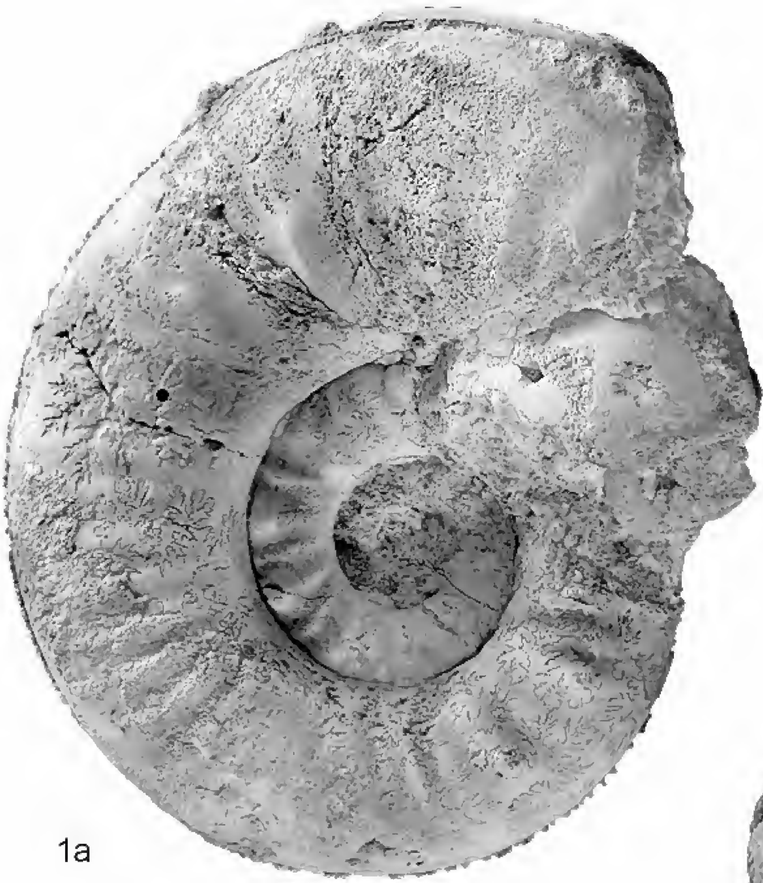
3b

Plate 2

Fig. 1. *Sonninia* aff. *adicra* (WAAGEN) [M]. Bed 8 b(ii); SM X40323.

Fig. 2. *Sonninia pseudotrigonata* MAUBEUGE. Wholly septate with no apparent simplification or approximation of the last visible sutures, hence probably [M] (cf. Pl. 1, Fig. 3). Bed 8 b(ii); SM X40324.

All figures natural size. Black spots on lateral views indicate the beginning of the bodychamber at the last septum.



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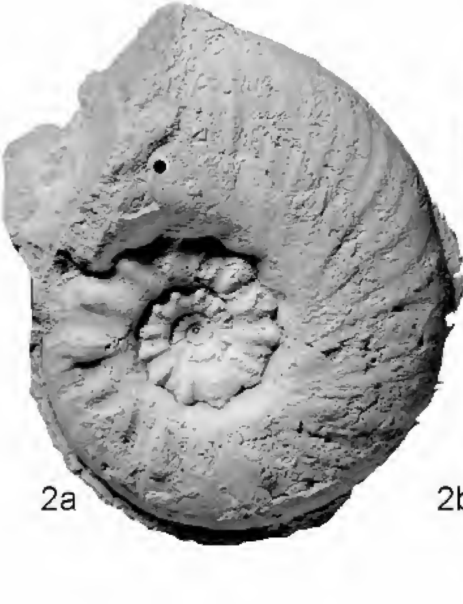

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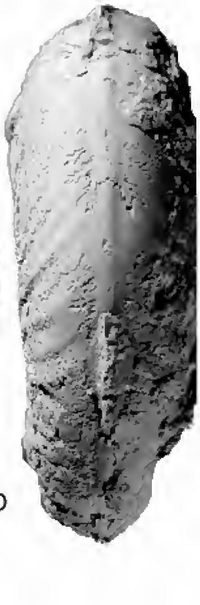

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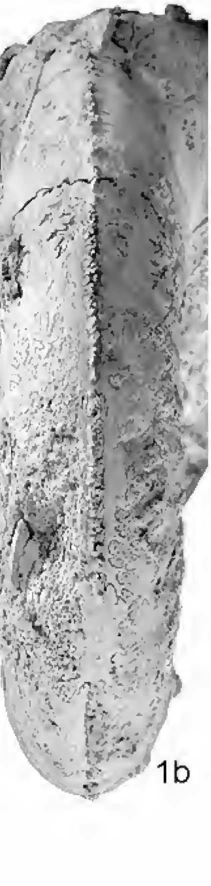

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Plate 3

Fig. 1. *Dundryites* aff. *albidus* Buckman [M], complete phragmocone. Note the complex sutureline. Bed 8 b(ii); SM X40325.

Fig. 2. *Dundryites albidus* Buckman [M], topotype, complete phragmocone, diameter 92 mm (the holotype is septate to 62 mm). Bed 8 b(i); SM X40326.

All figures natural size. Black spots on lateral views indicate the beginning of the bodychamber at the last septum.

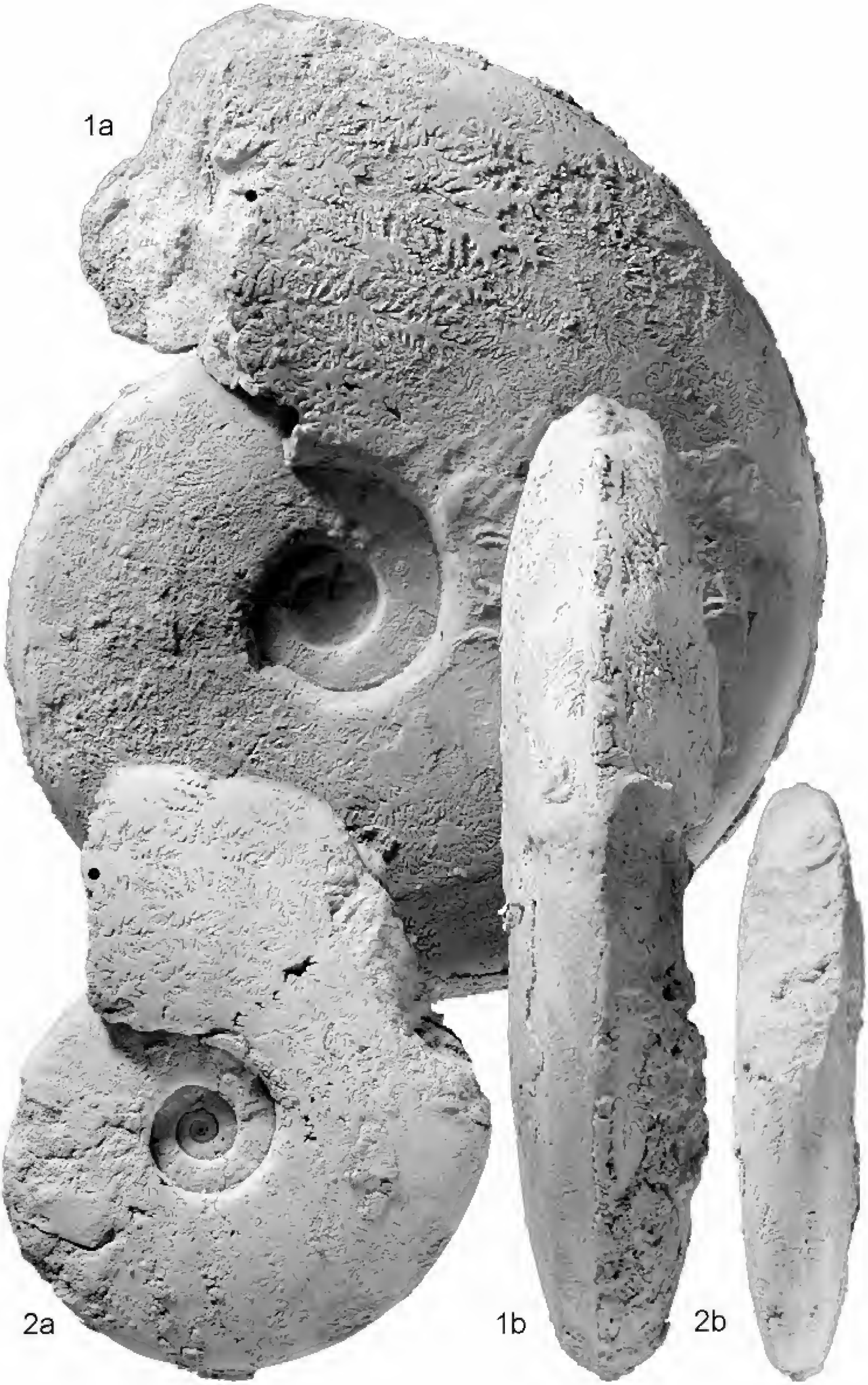
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Plate 4

Fig. 1. *Witchellia romanoides* (Douvillé) [M], typical example. Bed 8 a, ammonite faunal horizon of *Witchellia romanoides* (Bj-5); SM X40327.

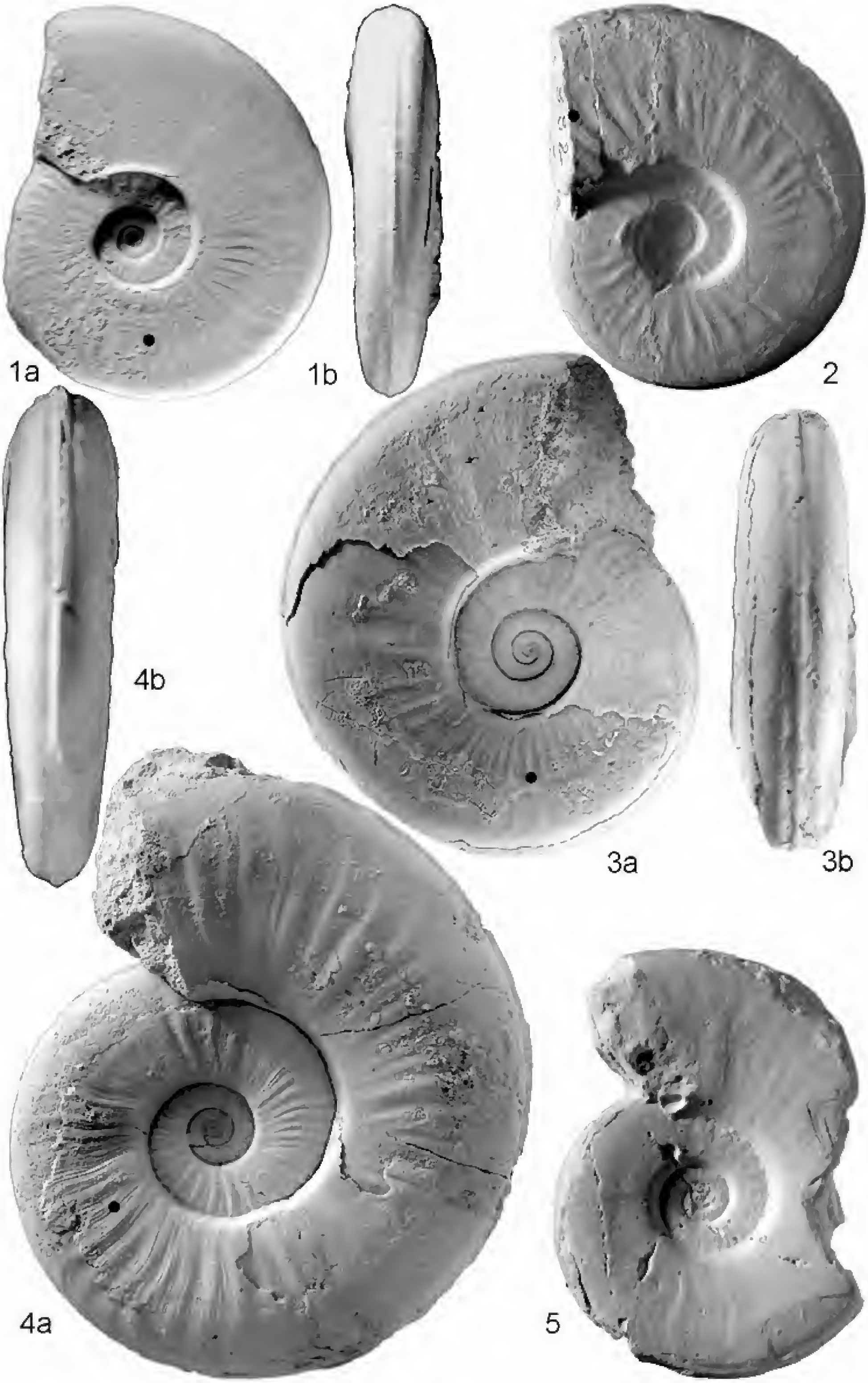
Fig. 2. *Witchellia romanoides* (Douvillé) [M], complete phragmocone. Cast of lectotype (designated here), Douvillé's syntype I (1885, pl. 3, fig. 4). 'Couche ocreuse, ?Ovale Zone of the Vallée de Valaury' (S France); SM X40330, Original STL EM 1705.

Fig. 3. *Witchellia romanoides* (Douvillé) [M], typical example. Bed 8 b(ii); SM X40328.

Fig. 4. *Witchellia romanoides* (Douvillé) [M], larger variant. Bed 8 b(i); SM X40329.

Fig. 5. *Witchellia romanoides* (Douvillé) [M], no sutures visible but the uncoiling umbilical sutures suggests a nearly complete adult. Cast of Douvillé's syntype II (1885, pl. 3, fig. 3), same locality and bed as Pl. 4, Fig. 2; SM X40331, Original STL EM 1702.

All figures natural size. Black spots on lateral views indicate the beginning of the bodychamber at the last septum.


1a
1b
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4b
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4a
5

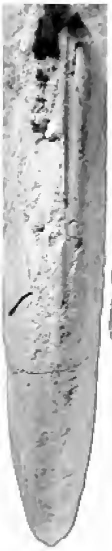
Plate 5

Fig. 1. *Witchellia* cf. *rubra* (BUCKMAN) [M], nearly complete. The type horizon of "*Rubrileiites*" *ruber* is in the upper part of the Laeviuscula Zone (Bj-9). Bed 8, loose; SM X40332.

Fig. 2. *Witchellia* cf. *jugifera* (WAAGEN). An adult, the last sutures strongly approximated: a variant of *W. romanoides* [M] or [m] of *jugifera*? Bed 8 a; SM X40323.

Fig. 3. *Witchellia jugifera* (WAAGEN) [M]. Cast of lectotype. Sowerbyi-Bank, ammonite faunal horizon of *Pseudoshirbuirnia oechslei* (Ovale Zone) of Gingen an der Fils (S Germany); SM X40324, Original BSPG AS XXII 36.

All figures natural size. Black spots on lateral views indicate the beginning of the bodychamber at the last septum.



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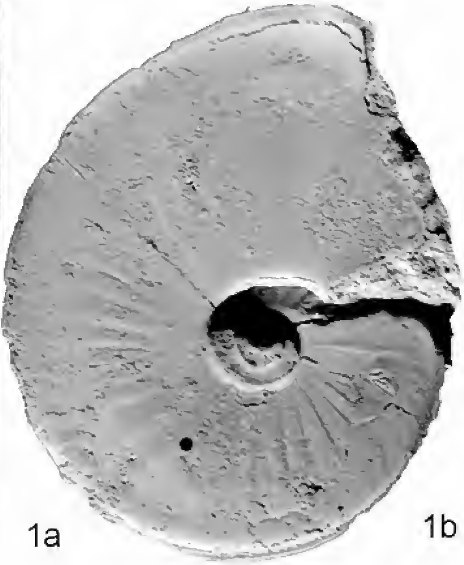

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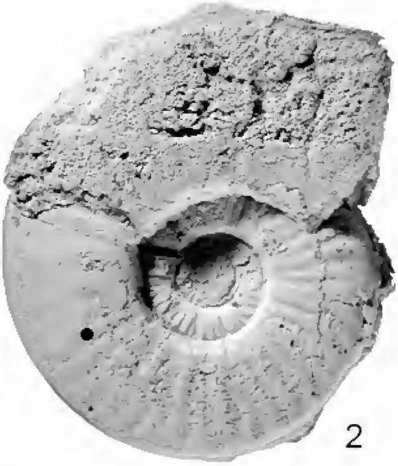

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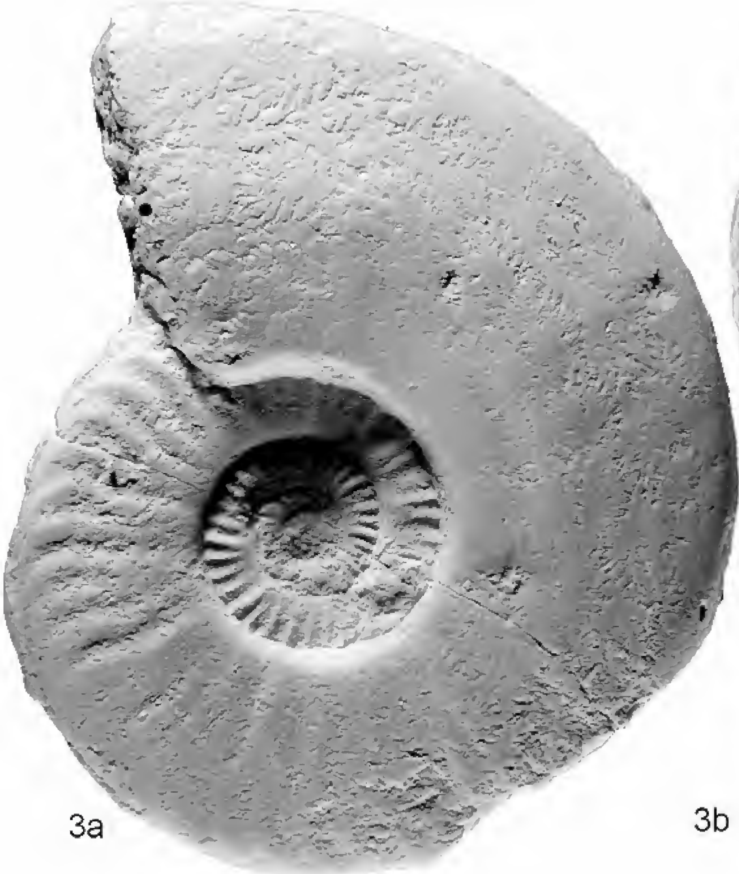

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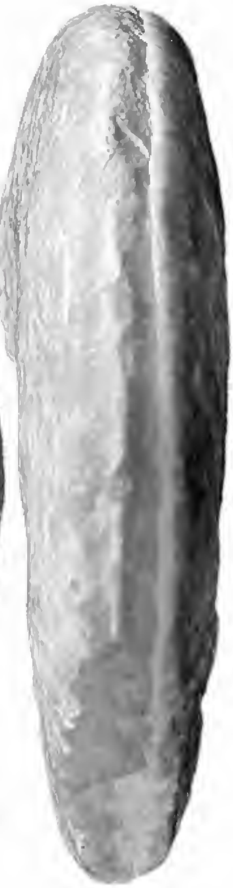

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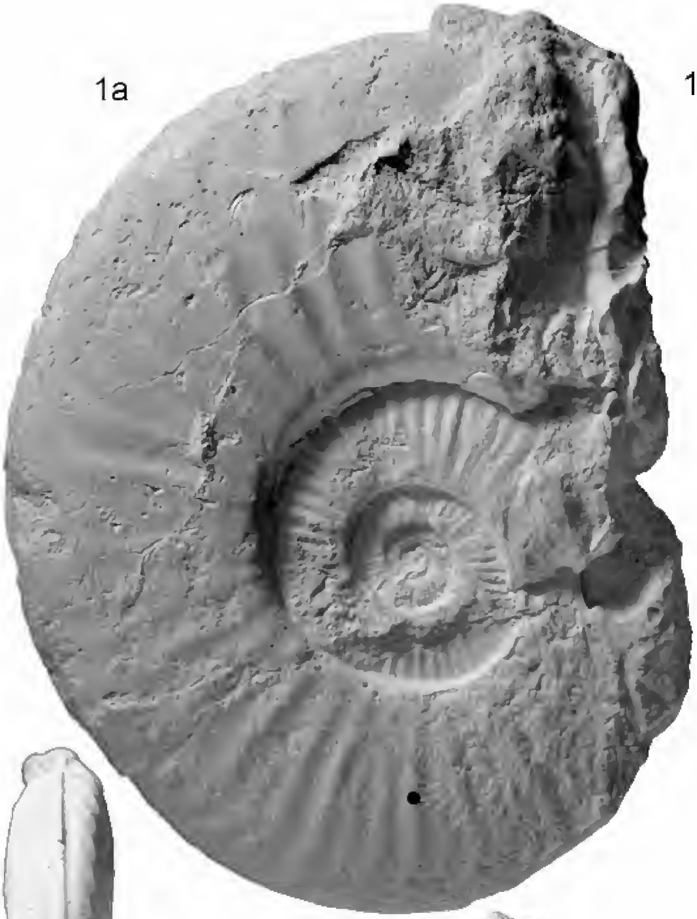
Plate 6

Fig. 1. *Witchellia sayni* HAUG [M]. Cast of lectotype (designated here, DOUVILLÉ 1885, pl. 2, fig. 1, 1a). Same source as *W. romanoides*, 'couche ocreuse, ?Ovale Zone of the Vallée de Valaury' (S France); SM X40335, Original STL EM 1719.

Fig. 2. *Witchellia* cf. *sayni* HAUG [M], adult, intermediate between *W. romanoides* and *W. sayni*. Bed 8 a; SM X40327.

Fig. 3. *Witchellia* cf. *zugophora* (BUCKMAN) [M], small adult variant with crowded last sutures. The type specimen of "*Zugophorites*" *zugophorus* is septate up to a diameter of about 108 mm, this specimen to 50 mm. It matches in sculpture the inner whorls of the type precisely: the main difference lies in the difference of sizes. This may reflect a form of ontogenetic polymorphism – see text. Bed 8 b(i); SM X40328.

All figures natural size. Black spots on lateral views indicate the beginning of the bodychamber at the last septum.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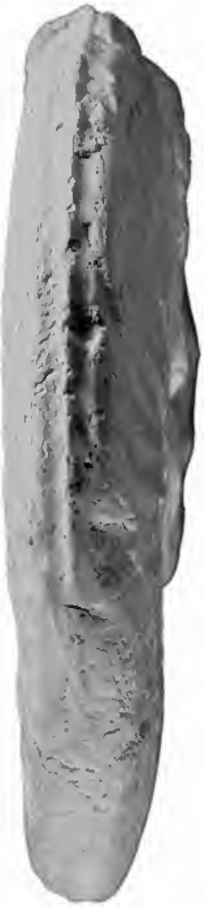
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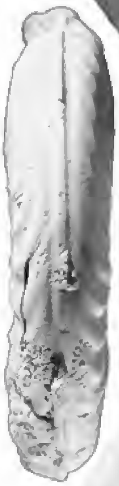
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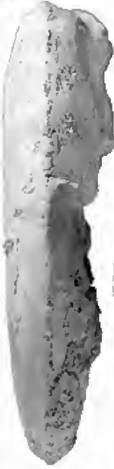
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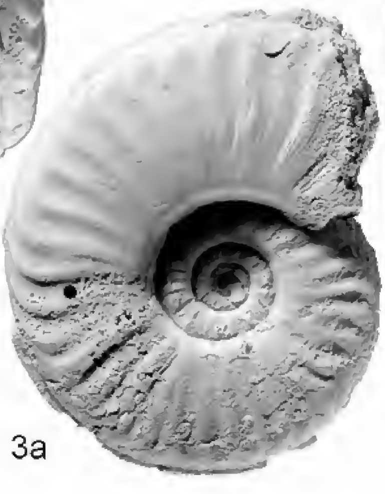
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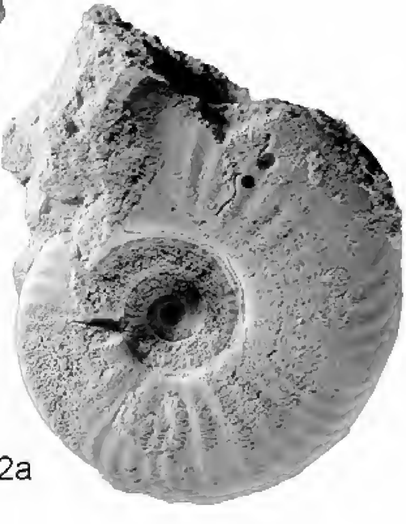
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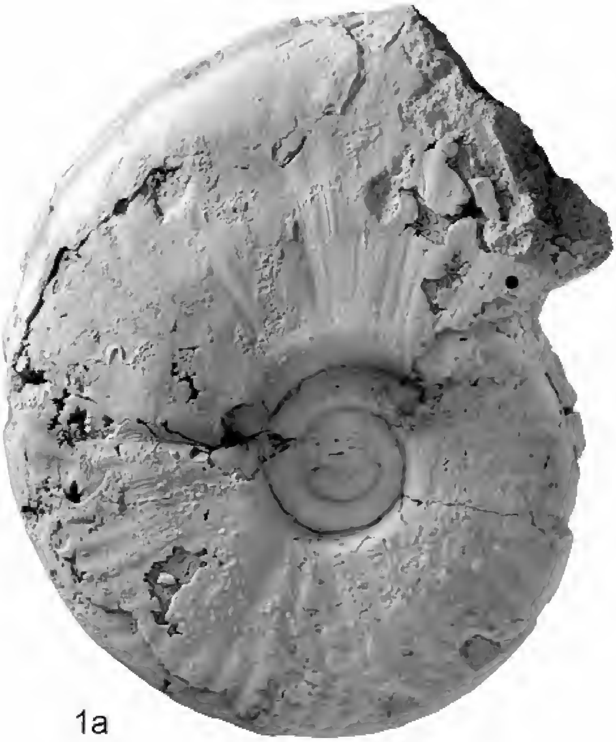
Plate 7

Fig. 1. *Witchellia* cf. *patefactor* (BUCKMAN) [M], partially preserved with test. The type horizon of *W. patefactor* lies at the top of the Laeviuscula Zone (probably Bj-10). Bed 8 b(ii); SM X40338.

Fig. 2. *Witchellia pavimentaria* (BUCKMAN) [M]. Bed 8, loose; SM X40339.

All figures natural size. Black spot on lateral view indicates the beginning of the bodychamber at the last septum.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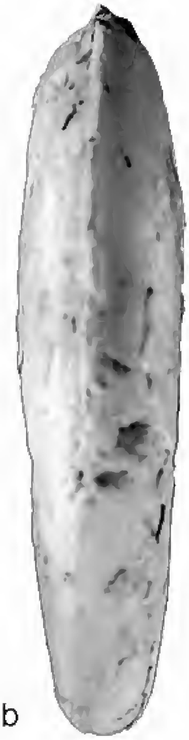
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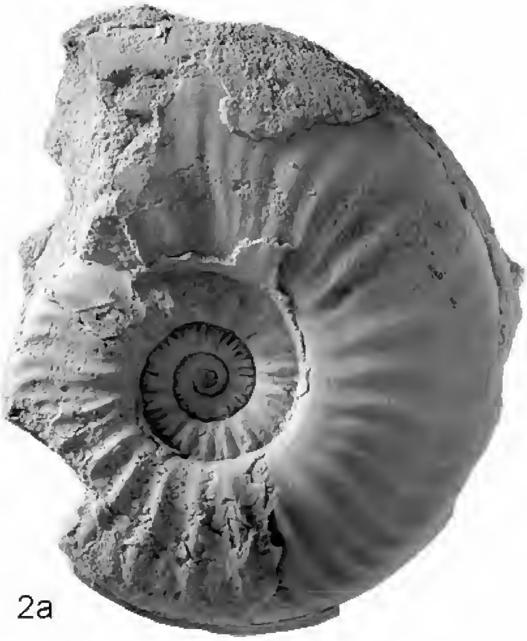
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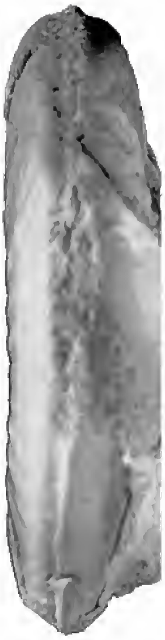
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Plate 8

Fig. 1. *Fissilobiceras ovale* (QUENSTEDT) [M]. Nearly complete adult, maximum diameter 340 mm; note the fissilobate septal suture. Similar giants – some with more rounded umbilical walls and then assigned to *F.* **fissilobatum* (WAAGEN) – occur throughout the whole of bed 8. Bed 8 b(i); SM X40340.

Fig. 2. *Fissilobiceras ovale* (QUENSTEDT) [M]. Wholly septate inner whorls, for comparison with Pl. 8, Fig. 1. Bed 8 a (–45/–50 cm); SM X40341.

All figures reduced × 0.5. Black spots on lateral views indicate the beginning of the body-chamber at the last septum.

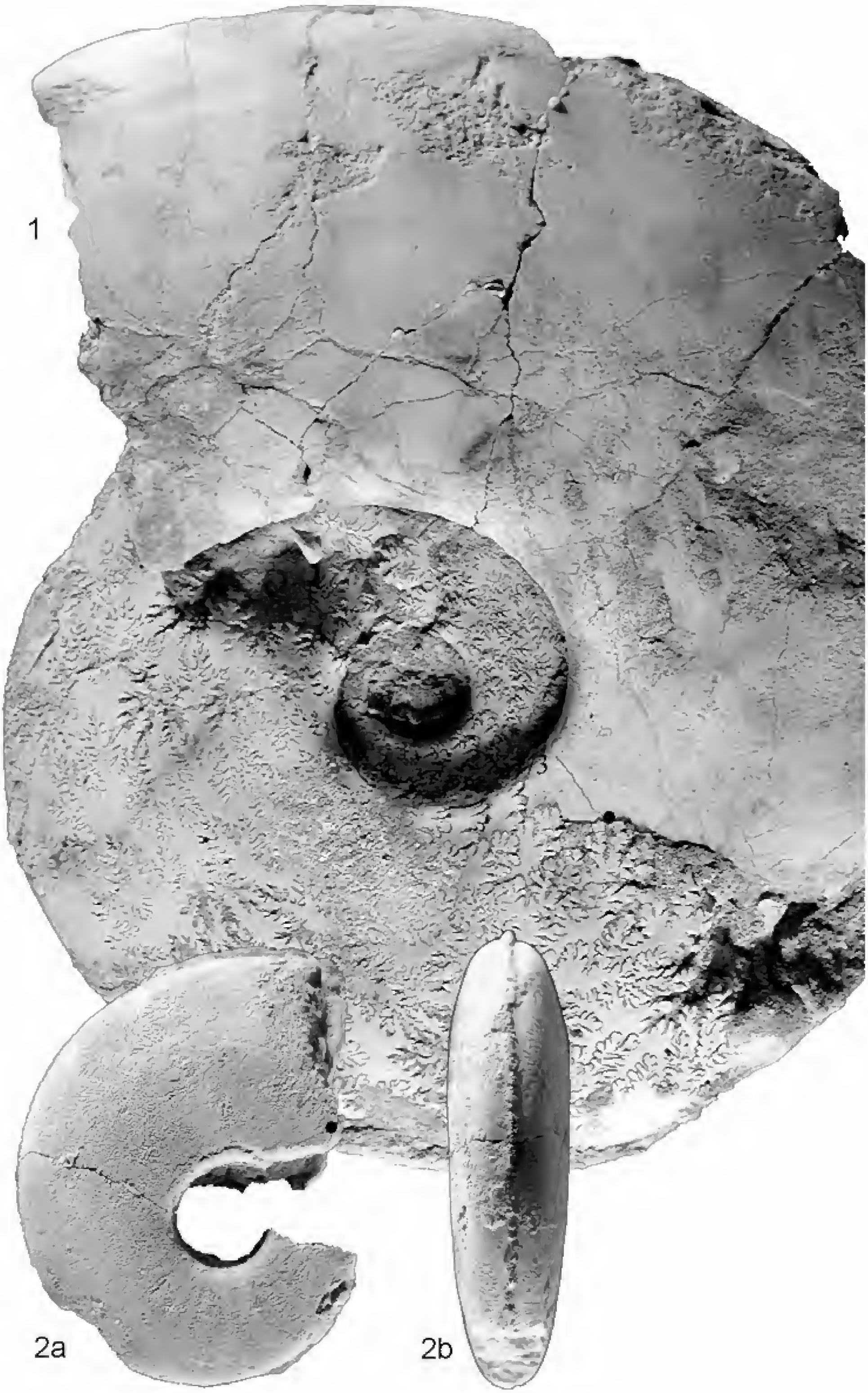
1
2a
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Plate 9

Fig. 1. *Emileia (Emileites) malenotata* (Buckman) [M]. Incomplete phragmocone with part of the bodychamber. The inner whorls exactly match the holotype of *Emileites malenotatus* Buckman (1927, TA 6, pl. 702), which is an incomplete phragmocone. Bed 8 b(ii); SM X40342.

Fig. 2. *Emileia (Emileites) malenotata* (Buckman) [M]. Complete phragmocone. Bed 8 b(ii); SM X40343.

Fig. 3. "*Emileites*" [gen. nov.] *liebi* Maubeuge [M]. Nearly complete specimen with some bodychamber. Compare the coronate bodychamber and accentuated primary ribbing at mid-whorl seen in this species with the more planulate coiling seen in *E. malenotata* (Pl. 9, Figs. 1–2), the bodychamber carrying long primary ribbing that fades (see text). Bed 8 b(i); SM X40344.

Fig. 4. "*Emileites*" [gen. nov.] *liebi* Maubeuge [M]. Complete and perhaps reworked specimen with nearly complete bodychamber. Bed 8 b(i); SM X40345.

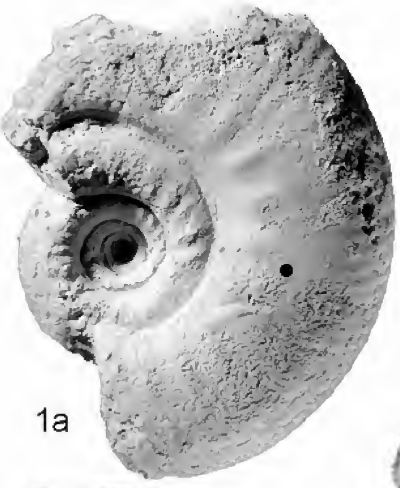
Fig. 5. "*Emileites*" [gen. nov.] *liebi* Maubeuge [M]. Complete but juvenile specimen of a coronate and small variant with a broader whorl-section. Bed 8 a; SM X40346.

Fig. 6. "*Trilobiticeras*" [gen. nov.] *cricki* Parsons [m]. Complete specimen of a small variant with lappets. Note the coronate stage with the prominent primary ribbing on the lateral edge of the whorls up to the bodychambers in Figs. 6–8, resembling that in "*Emileites*" *liebi* [M], the supposed sexual dimorphic counterpart. Bed 8 a; SM X40347.

Fig. 7. "*Trilobiticeras*" [gen. nov.] *cricki* Parsons [m]. Larger variant, complete with lappets. Bed 8 b(ii); SM X40348.

Fig. 8. "*Trilobiticeras*" [gen. nov.] *cricki* Parsons [m]. Another complete specimen with lappets. Bed 8 b(ii); SM X40349.

All figures natural size. Black spots on lateral views indicate the beginning of the bodychamber at the last septum.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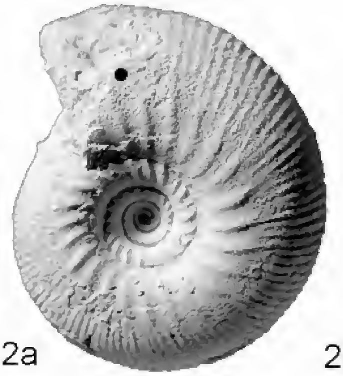
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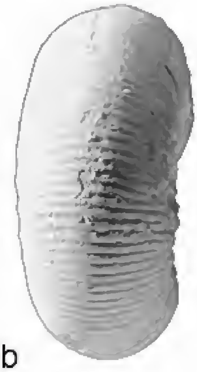
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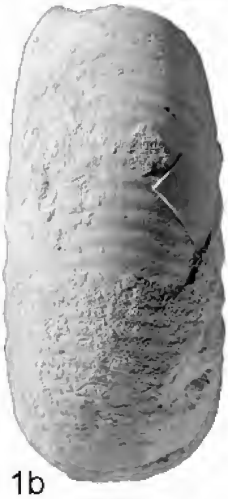
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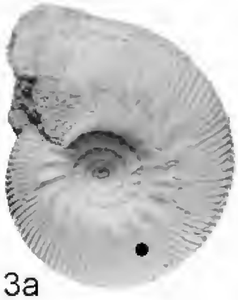
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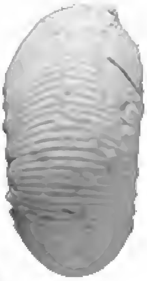
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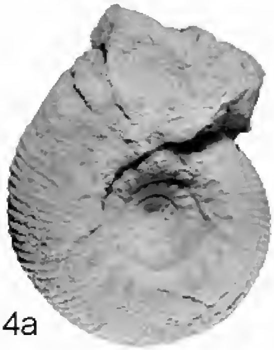
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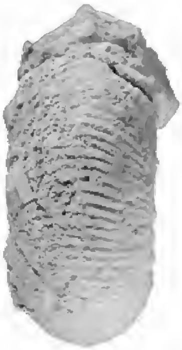
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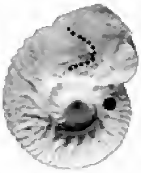
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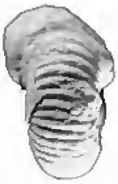
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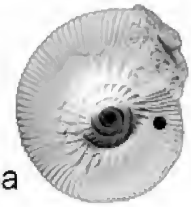
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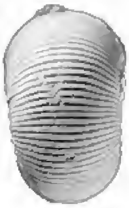
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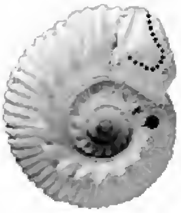
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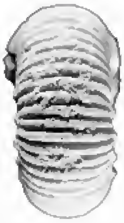
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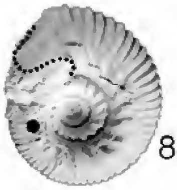
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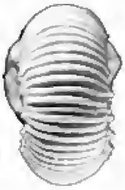
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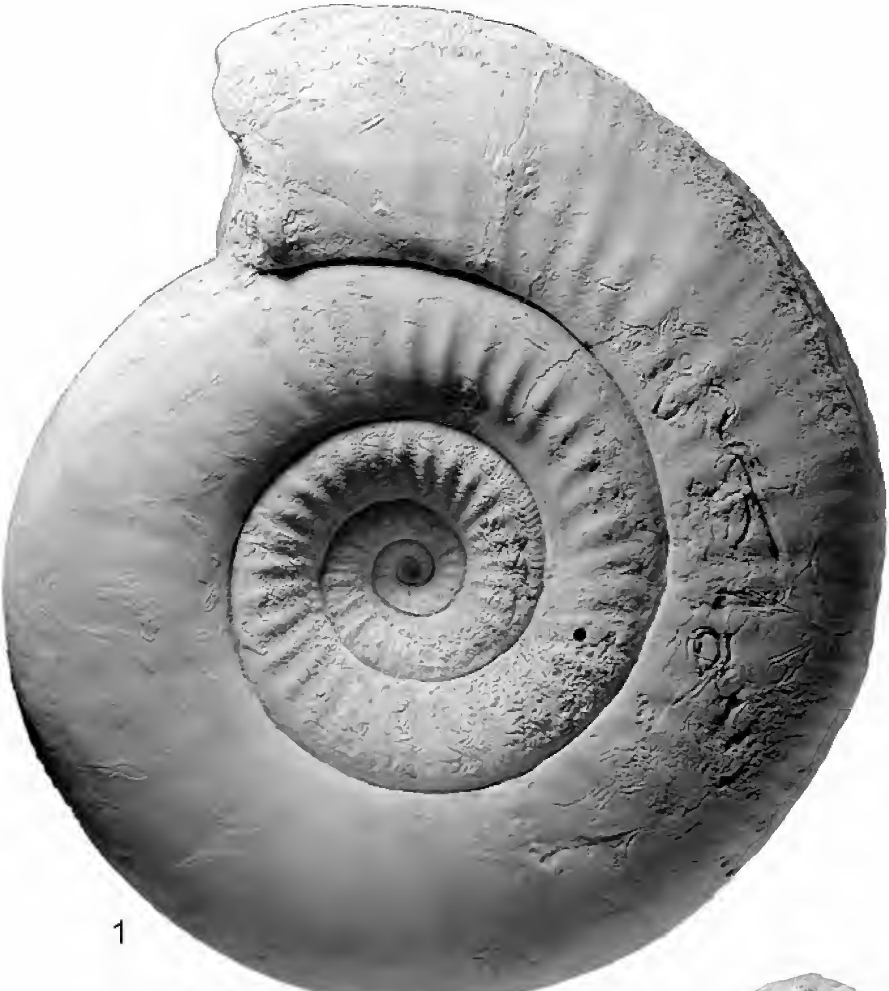
Plate 10

Fig. 1. *Emileia (Emileia)* aff. *dundriensis* Callomon & Chandler [M]. The first half of the last whorl of the bodychamber is artificial; maximum diameter 250 mm. The inner whorls are slightly more coronate and the coiling still more evolute than in the bulk of the type material of *E. dundrienis*, from the Trigonalis Subzone of the Laeviuscula Zone. Gift from J. Huxtable to one of the authors (V. D.); by preservation from bed 8 b(ii); SM X40350. For ventral view, see Pl. 11, Fig. 2. – Reduced × 0.5.

Fig. 2. *Otoites douvillei* Parsons [m]. Complete specimen with lappets. Bed 8 b(ii); SM X40351. – Natural size.

Fig. 3. *Otoites tumulosus* Westermann [m]. Nearly complete specimen lacking the peristome. In contrast to the small *O. douvillei*, which is restricted to the Ovale and lowermost Laeviuscula Zone, the larger forms like *O. tumulosus* range into the Sauzei Zone. Bed 8 b(ii); SM X40352. – Natural size.

Black spots on lateral views indicate the beginning of the bodychamber at the last septum.



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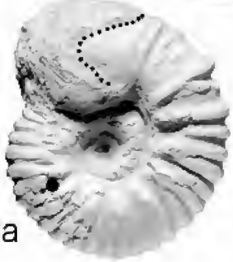

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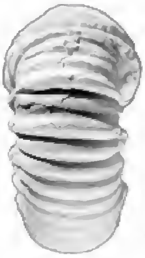

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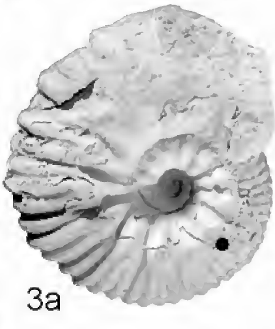

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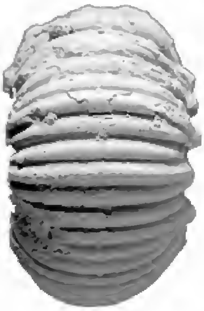

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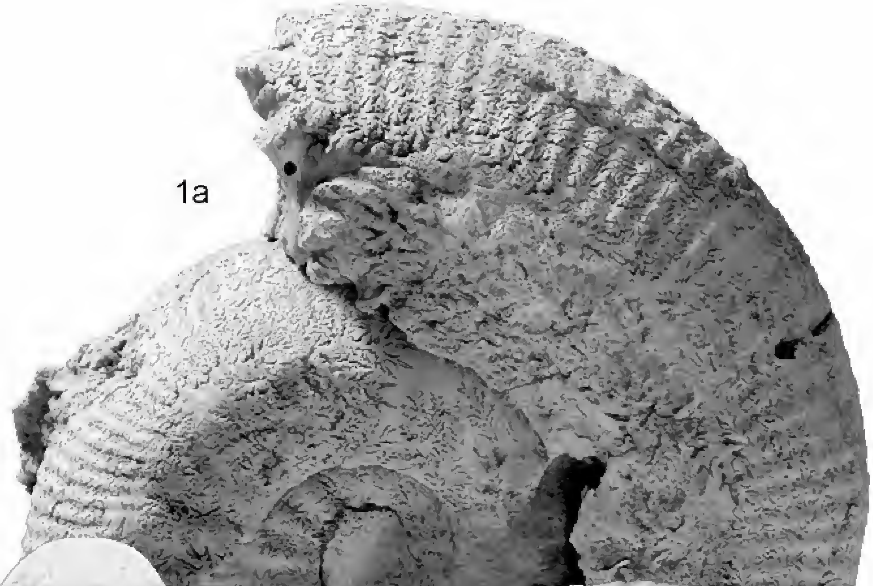
Plate 11

Fig. 1. *Emileia (Emileia) dundriensis* Callomon & Chandler [M]. Incomplete phragmocone. Bed 8 b(ii); SM X40353. – Natural size.

Fig. 2. *Emileia (Emileia)* aff. *dundriensis* Callomon & Chandler [M], ventral view of specimen shown on Pl. 10, Fig. 1; SM X40350. – Reduced × 0.5.

Black spot on lateral view indicates the beginning of the bodychamber at the last septum.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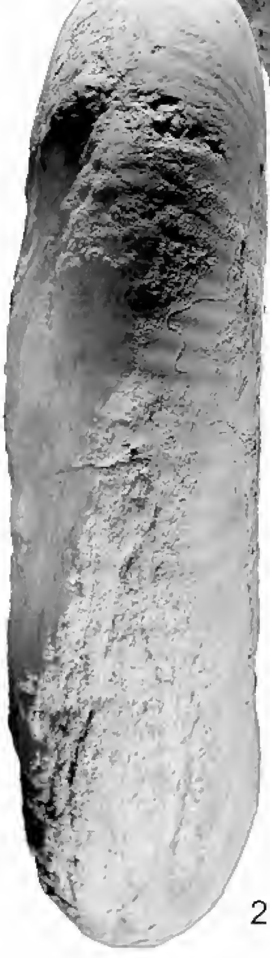
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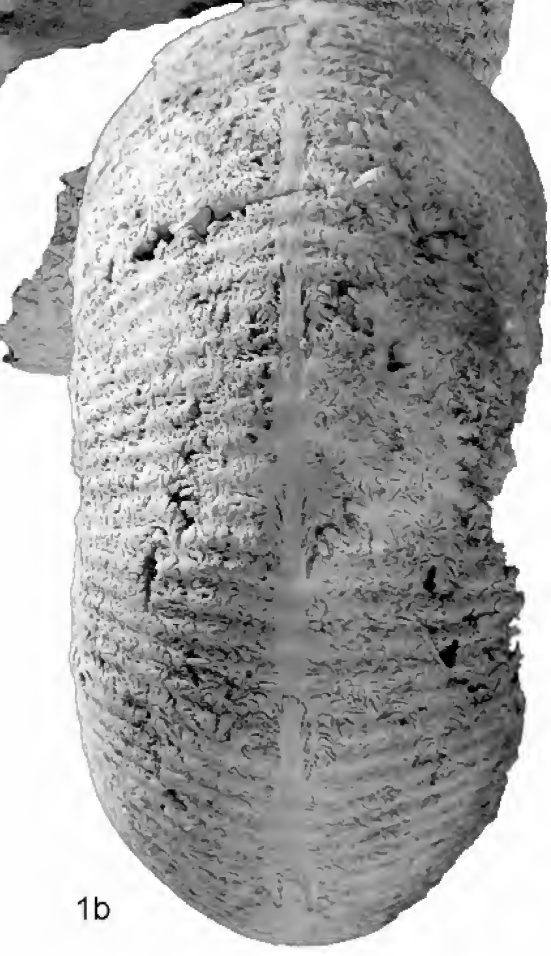
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The petasma of *Antrimpos undenarius* Schweigert (Crustacea: Penaeidae) from the Nusplingen Lithographic Limestone (Upper Jurassic, SW Germany)

Das Petasma von *Antrimpos undenarius* Schweigert (Crustacea: Penaeidae) aus dem Nusplinger Plattenkalk (Oberjura, Südwestdeutschland)

Hermann Polz

Abstract

The petasma of *Antrimpos undenarius* Schweigert is compared with the petasmata of *A. speciosus* Münster and "*Penaeus*" *meyeri* Oppel, and recognized as an important distinctive feature. In contrast to the petasma of *A. undenarius* with its long lateral lobe, distally forming a large gentle hook, thus ventral costa strongly curved, *A. speciosus* Münster shows a petasma with a lateral lobe distolaterally produced into a small auriculate, flaplike projection. The petasma of "*Penaeus*" *meyeri* Oppel differs markedly by its lateral lobe, distally increasing in width and terminating in a thin, dorsally broadened spatual- to shovelshaped and presumably flexible part.

Nomenclatural changes of Münster's genera *Antrimpos* and *Koelga* are listed.

Keywords: Upper Jurassic, Upper Kimmeridgian, Nusplingen, *Antrimpos undenarius*, *Antrimpos speciosus*, "*Penaeus*" *meyeri*, petasma.

Zusammenfassung

Das Petasma von *Antrimpos undenarius* Schweigert wird mit den Petasmata von *A. speciosus* Münster und „*Penaeus*" *meyeri* Oppel verglichen und als wichtiges artspezifisches Unterscheidungsmerkmal vorgestellt. Im Gegensatz zum Petasma von *A. undenarius* mit seinem langen Seitenstrang (lateral lobe), der distal einen großen Haken bildet, wodurch die ventrale Rippe kräftig gebogen ist, besitzt *A. speciosus* Münster ein Petasma, dessen lateral lobe distolateral eine ohrenförmige, lappenartige Ausbuchtung zeigt. Das Petasma von „*P.*" *meyeri* unterscheidet sich ausgesprochen deutlich von den beiden vorigen, indem es in einem breiten dorsal ausgerichteten, spatel- bis schaufelförmigen, vermutlich flexiblen Abschnitt endet.

Nomenklatorische Änderungen bei den Münster'schen Gattungen *Antrimpos* und *Koelga* werden aufgelistet.

1. Introduction

Morphology of the reproductive structures is one of the key characters in crustaceans. The structure of gonopods in the Decapoda (e. g. KLAUS et al. 2006) has proved to be a helpful feature for gender- as well as for species-identification, and is equally important in phylogeny. In male Dendrobranchiata the characteristic secondary sexual structure is called the petasma (DALL et al. 1990, BAUER 1991, PÉREZ FARFANTE & KENSLEY 1997). It is a specialised appendage developed by modification of the hypothetical basic pattern of the uniform appendages of Crustacea. This also concerns male Penaeoidea, where the endopods of the first pair of abdominal appendages are coupled and changed into a folded to tubular shape (Pl. 2, Figs. 1 and 2).

In fossil crustaceans the discovery of clear identification characters is particularly welcome. The preservation of fossil petasmata is usually poor, even when they are discernible, and their state of preservation does not permit comparison with the condition of this character in living animals. Nevertheless, this external identification structure has already been applied in the systematic and phylogenetic interpretation of Penaeoidea from the Solnhofen Lithographic Limestones (POLZ 2002, 2003).

The Nusplingen Lithographic Limestone is a plattenkalk, approximately 0.5 million years older than that of Solnhofen. It is of Late Kimmeridgian age and the source of numerous crustaceans, more than 80 % representing the prawn genus *Antrimpos* (SCHWEIGERT 2001: 15). On account of morphological differences SCHWEIGERT (2001) erected the new species *A. undenarius*. Recently, in another case of excellent preservation from this site, a specimen of this species has been found to exhibit a well preserved petasma, which is described in this study.

Acknowledgements

Thanks are due to Dr. GÜNTER SCHWEIGERT, Stuttgart, who encouraged to the author to report on this find. The Staatliches Museum für Naturkunde Stuttgart (SMNS) made available the specimen for this study. I am also indebted to Dr. W. D. I. ROLFE, Edinburgh, who provided valuable comments and kindly improved the English. Dr. G. SCHWEIGERT, Stuttgart, Dr. A. GARASSINO, Milan, and Dr. R. BÖTTCHER, Stuttgart, reviewed the manuscript and gave helpful comments.

2. Material

Among many other fossils found during the 2005 excavation in the Upper Kimmeridgian Nusplingen quarry was a specimen of *Antrimpos undenarius* with the petasma preserved. The thin slab containing the fossil comes from bed L, about 10 cm from top of the sequence (see section in DIETL et al. 1998).

Fossil shrimps and prawns are usually embedded in lateral position due to their lateral compression. Although this partly disintegrated specimen shows a nearly complete dorsal aspect, the petasma is not hidden underneath the body but has been displaced outside the first abdominal somite. The partial disintegration, especially of the appendages, may result from the circumstance that the animal was embedded with its back on the sediment layer, exposing the venter to various influences. Most of sixth abdominal somite and the tailfan are not available, as part of the slab is missing (Fig. 1).

The specimen was prepared mechanically by the author, and is now housed in the collection of the SMNS, no. 66122.

3. Description

The studied specimen exhibits a well preserved left half, and the lateral lobe of the right half, of the petasma (Fig. 1). Presumably on account of partial disintegration and external mechanical effects, the petasma seems to be embedded in a turned position. The inner surface of the left half is visible now with the ventral margin directed anteriorly (Fig. 2). The lateral aspect (ventral part below) is sketched in Fig. 3A and B. Length is at least 11 mm, width 4.6 mm.

General shape: marked distinguishing features in petasmata are above all the distal (distolateral, distomedian) projections, apical parts of various structures (Plate 2, Fig. 3a and b). In this specimen the ventral costa of the lateral lobe is long, strongly curved and thus apically forms a blunt dorsally-directed hook, extending beyond the apex of the median lobe; the latter is relatively large, the anterior margin having a distinct medial concavity, the lobe terminating anteriorly in a blunt tip (Fig. 3A; Pl. 1, Figs. 1a and 2a).

Symmetry: a definite statement about this feature is not possible as only one half of the petasma is available. However, by chance the disintegrated lateral lobe of the second half of the petasma is preserved near by (Pl. 1, Figs. 1b and 2b). It is of the same shape as the corresponding part in the left half of the petasma, and therefore it is to be supposed that the petasma is a symmetrical one (PÉREZ FARFANTE & KENSLEY (1997): 24 of 26 listed penaeid genera have symmetrical petasmata; Tab. 1).

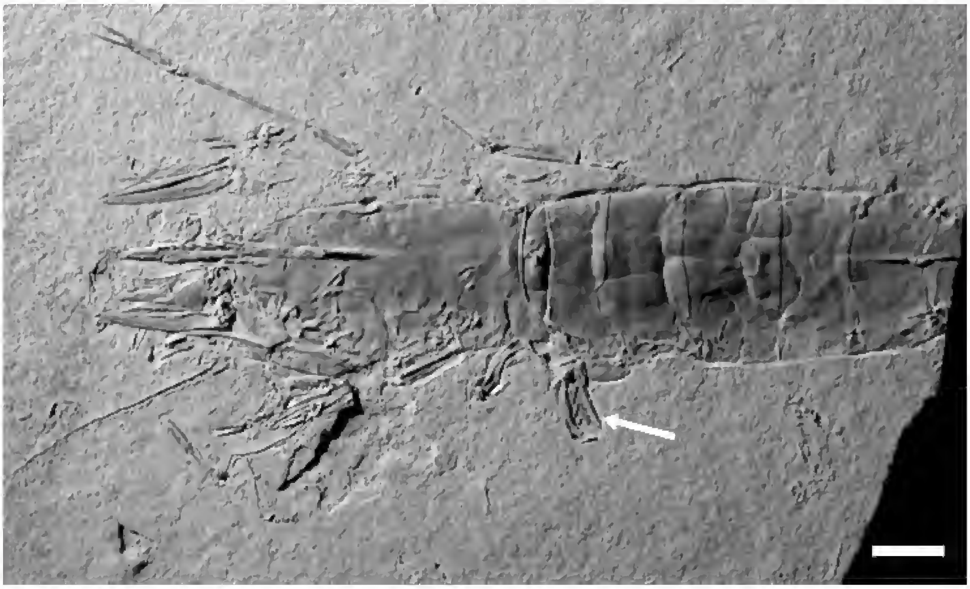

Fig. 1. *Antrimpos undenarius* SCHWEIGERT, with preserved petasma (→); Nusplingen Lithographic Limestone, Nusplingen quarry, bed L, Upper Kimmeridgian, Beckeri Zone, Ulmense Subzone. SMNS 66122. – Scale bar 1 mm.

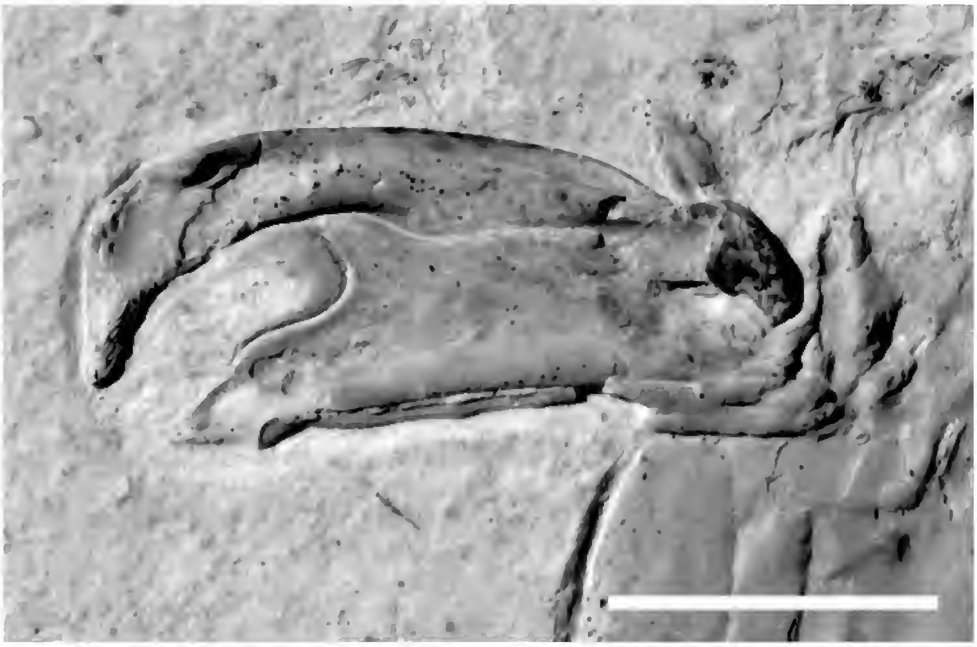

Fig. 2. *Antrimpos undenarius* SCHWEIGERT. Petasma enlarged from Fig. 1. – Scale bar 5 mm.

Closure: only three-dimensional preservation would permit certainty but, compared with the semiclosed petasma of *Fenneropenaeus indicus* (H. MILNE EDWARDS) (Pl. 2, Fig. 3b), the present petasma could be a semiclosed one, too. Usually penaeid petasmata are semiclosed (PÉREZ FARFANTE & KENSLEY (1997): 20 of 26 listed penaeid genera have semiclosed petasmata; Tab. 1).

Sclerotization: to verify whether the lateral lobes of a petasma are more or less flexible or sclerotised is possible in extant species but in fossils it is reduced to the comparison of its shape with similar forms in living animals (Pl. 2). As the present

Tab. 1. Petasma characters in living Penaeidae drawn up from details in PÉREZ FARFANTE & KENSLEY 1997.

	Artemisia	*Atypopenaeus*	*Farfantepenaeus*	*Fenneropenaeus*	*Funchalia*	*Heteropenaeus*	*Litopenaeus*	*Macropetasma*	*Marsupenaeus*	*Megokris*	*Melicertus*	*Metapenaeopsis*	*Metapenaeus*	*Miyadiella*	*Parapenaeopsis*	*Parapenaeus*	*Pelagopenaeus*	*Penaeopsis*	*Penaeus*	*Protrachypene*	*Rimapenaeus*	*Tanypenaeus*	*Trachypenaeopsis*	*Trachypenaeus*	*Trachysalambria*	*Xiphopenaeus*
symmetrical	×	×	×	×		×	×	×	×	×	×		×	×	×	×	×	×	×	×	×	×	×	×	×	×
asymmetrical					×							×														
semiopen					×	×	×							×			×									
semiclosed	×	×	×	×				×	×	×	×		×		×	×		×	×	×	×	×	×	×	×	×

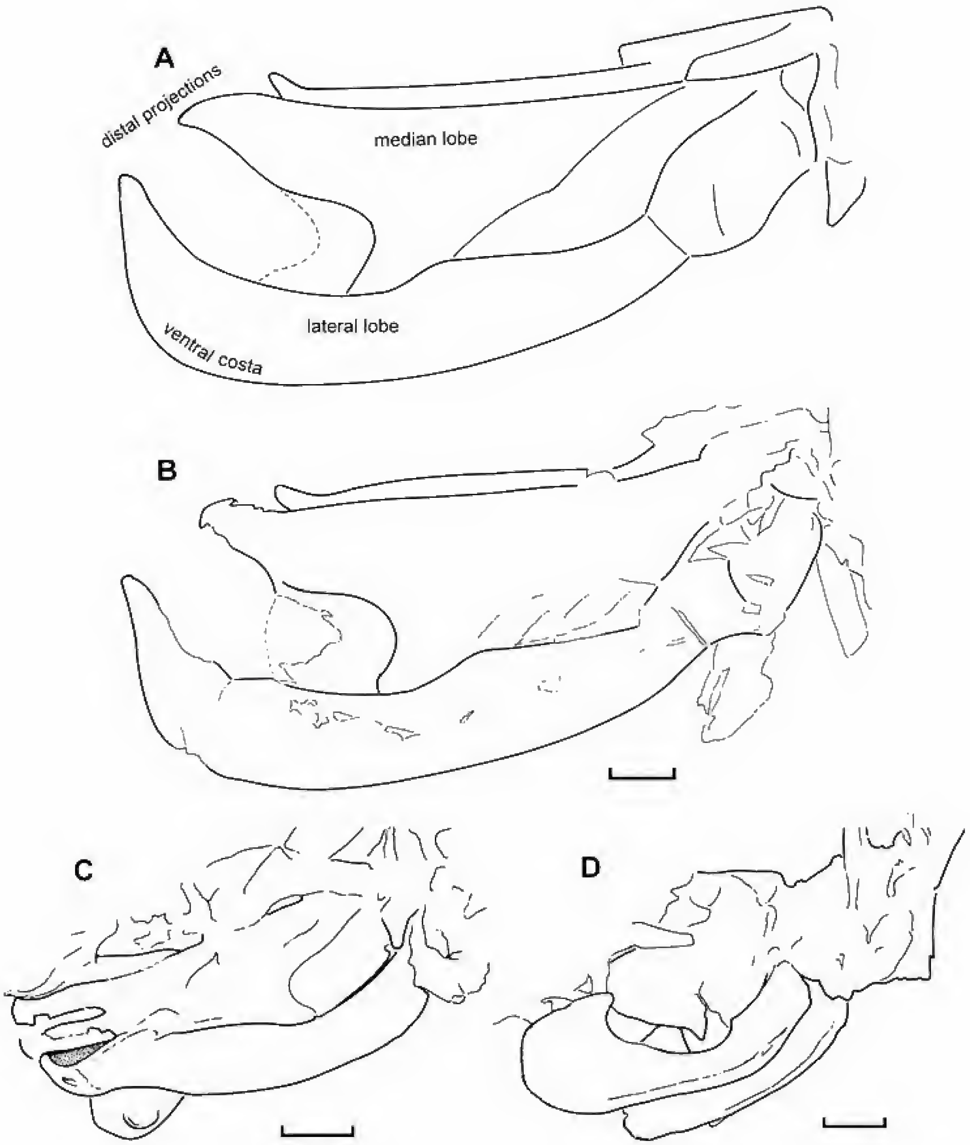

Fig. 3. Comparison of petasmata. **A**: *Antrimpos undenarius* Schweigert; diagrammatic sketch with tentatively assigned terms used in penaeid taxonomy. **B**: *Antrimpos undenarius* Schweigert, (mirrored); Nusplingen Lithographic Limestone, Nusplingen quarry, bed L, Upper Kimmeridgian, Beckeri Zone, Ulmense Subzone; SMNS 66122. **C**: *Antrimpos speciosus* Münster; Solnhofen Lithographic Limestones, Lower Tithonian; author's collection no. 99032103. **D**: "*Penaeus*" *meyeri* Oppel; Solnhofen Lithographic Limestones, Lower Tithonian; author's collection no. 94061601. C and D slightly altered after Polz 2002. – Scale bars 1 mm.

petasma seems to be as well preserved as the cephalothorax or the abdominal somites, it must have been considerably sclerotized.

Tab. 2. Penaeid species from the South German Jurassic Plattenkalks referred by Münster (1839) to his genera *Antrimpos* and *Koelga*, and their nomenclatural changes by selected subsequent authors. Münster (1839: 61, 62) mentioned in his description of *Koelga laevirostris* the name "*Squilla*?", referring to Baier's *Squilla gibba* from 1757 (as pre-Linnean not valid). However, he did not indicate any reference to another taxon when describing *Koelga gibba*, thus, there is no connection with Baier's species name "*gibba*".

Baier 1757	Walch 1773	Münster 1839	Quenstedt 1852	O. Fraas 1855	Quenstedt 1858	Oppel 1862	Walther 1904
	Locusta marina	***Antrimpos speciosus***	*Penaeus speciosus* (Münster)	*Penaeus speciosus* (Münster)	*Penaeus speciosus* (Münster)	*Penaeus speciosus* (Münster)	*Penaeus speciosus* (Münster)
		Antrimpos angustus	*Penaeus speciosus* (Münster)			*Penaeus speciosus* (Münster)	
		Antrimpos bidens	?*Penaeus speciosus* (Münster)			*Penaeus speciosus* (Münster)	
		Antrimpos decemdens	*Penaeus speciosus* (Münster)			*Penaeus speciosus* (Münster)	
		Antrimpos nonodon				*Penaeus speciosus* (Münster)	
		Antrimpos tridens				*Penaeus intermedius*	*Penaeus intermedius* Oppel
		Antrimpos trifidus				*Penaeus speciosus* (Münster)	
		Antrimpos senidens				*Penaeus meyeri*	*Penaeus meyeri* Oppel
		?***Antrimpos dubius***				*Penaeus intermedius*	
	Squilla	***Koelga quindens***	?*Penaeus speciosus* (Münster)			*Penaeus speciosus* (Münster)	
		Koelga gibba (after Schweigert 2001 nom. dub.)		*Penaeus speciosus* (Münster)	*Penaeus speciosus* (Münster)	*Penaeus speciosus* (Münster)	*Penaeus speciosus* (Münster)
		Koelga septidens				*Penaeus speciosus* (Münster)	
Squilla gibba		***Koelga laevirostris***				*Penaeus speciosus* (Münster)	
		Koelga quadridens				*Penaeus meyeri*	*Penaeus meyeri* (Oppel)
		Koelga curvirostris					
		Koelga dubia				*Penaeus meyeri*	
		Koelga tridens				*Penaeus meyeri*	

Tab. 2. Continuation.

Engel 1908	E. Fraas 1910	Balss 1922	van Straelen 1925	Glaessner 1929	Dietl et al. 2000	Schweigert 2001	Schweigert & Garassino 2004
		Penaeus speciosus (Münster)	*Antrimpos speciosus* Münster	*Antrimpos speciosus* Münster			
			Antrimpos speciosus Münster	*Antrimpos speciosus* Münster			
			Antrimpos speciosus Münster	*Antrimpos speciosus* Münster			
			Antrimpos speciosus Münster	*Antrimpos speciosus* Münster			
			Antrimpos speciosus Münster	*Antrimpos speciosus* Münster			
		Penaeus intermedius Oppel	*Antrimpos intermedius* (Oppel)	*Antrimpos intermedius* (Oppel)			
			Antrimpos speciosus Münster	*Antrimpos speciosus* Münster			
		Penaeus meyeri Oppel	*Antrimpos meyeri* (Oppel)	*Antrimpos meyeri* (Oppel)			
			Antrimpos intermedius (Oppel)	*Antrimpos intermedius* (Oppel)			
			Antrimpos speciosus Münster	*Antrimpos speciosus* Münster			
Penaeus speciosus (Münster)	*Penaeus speciosus* (Münster)		*Antrimpos speciosus* Münster	*Antrimpos speciosus* Münster	*Antrimpos* aff. *speciosus* Münster	***Antrimpos undenarius*** Schweigert	
			Antrimpos speciosus Münster	*Antrimpos speciosus* Münster			
			Antrimpos speciosus Münster	*Antrimpos speciosus* Münster			
		Penaeus meyeri (Oppel)	*Antrimpos meyeri* (Oppel)	*Antrimpos meyeri* (Oppel)			
				?*Drobna curvirostris* (Münster)			*Koelga curvirostris* Münster
			Antrimpos meyeri (Oppel)	*Antrimpos meyeri* (Oppel)			
			Antrimpos meyeri (Oppel)	*Antrimpos meyeri* (Oppel)			

4. Petasmata as distinguishing features in MÜNSTER's genera *Antrimpos* and *Koelga*

Fossil crustaceans which at present are referred to the genus *Antrimpos* MÜNSTER have undergone numerous nomenclatural changes since their first publication, partially depending on different estimation of their characters (Tab. 2). Discovering petasmata is therefore useful in discriminating them taxonomically.

The genera *Antrimpos* and *Koelga* were established by MÜNSTER (1839) comprising nine and eight species respectively, including nomina dubia: *Antrimpos speciosus*, the type species, designated by WOODS (1925), *A. angustus*, *A. bidens*, *A. decemdens*, *A. nonodon*, *A. tridens*, *A. trifidus*, *A. senidens*, and ?*A. dubius*, and *Koelga curvirostris*, as type species designated by SCHWEIGERT & GARASSINO (2004), *K. dubia*, *K. gibba*, *K. laevirostris*, *K. quadridens*, *K. quindens*, *K. septidens*, and *K. tridens*. He suggested crustaceans formerly mentioned by BAIER (1757) and WALCH (1773) as species of his new erected genera. BAIER dealt with fossils of his father's collection, among them "*Squilla gibba*", while WALCH divided his fossils into groups with or without bones. Among boneless animals he listed "Gamarrholithen und Trilobiten" as insects with a shell, including among others the crustaceans "*Locusta marina*" and "*Squilla*".

MÜNSTER (1839) pointed out the similarity of his genus *Antrimpos* to the modern genus *Penaeus* FABRICIUS, 1798, a similarity which induced OPPEL (1862), who considered a few of MÜNSTER's taxa to be nomina dubia, to synonymise the genus with *Penaeus*. He attributed MÜNSTER's *Antrimpos*- and *Koelga*-species from the Upper Jurassic to three species only: *Penaeus speciosus* (MÜNSTER), *P. intermedius* OPPEL, and *P. meyeri* OPPEL. VAN STRAELEN (1925) and GLAESSNER (1929) recognized only three of MÜNSTER's species in accepting OPPEL's revision and reactivating MÜNSTER's genus *Antrimpos*: *A. speciosus* MÜNSTER, *A. intermedius* (OPPEL), and *A. meyeri* (OPPEL).

DIETL et al. (2000) suggested the numerous fossil prawns from the Nusplingen Lithograpic Limestone were of *A. speciosus* affinity, only. Finally SCHWEIGERT (2001) described these finds as a closely related but separate form, differing from the type species above all by one more dorsal tooth in the rostrum, the eleventh. He therefore erected the species *undenarius*.

Further evidence of *A. undenarius* as a separate species is now furnished by the well preserved petasma of the find described herein. Petasmata, key features in Sergestoidea, are not only a means of distinguishing between the sexes but are also important species characters, as are the thelyca in females. The petasmata of *A. undenarius* and of two related penaeids from the South German Upper Jurassic clearly differ from each other in the shape of the distal parts of their lateral lobes (Fig. 3):

A. undenarius SCHWEIGERT (MÜNSTER's "*Koelga gibba*" is considered as a nomen dubium by SCHWEIGERT 2001: 12): lateral lobe long, distally turning upwards in an angle of about 60 degrees and forming a large gently-curved hook, with strongly curved ventral costa (Fig. 3 B).

A. speciosus MÜNSTER: lateral lobe distolaterally produced into a small auriculate, flaplike projection (Fig. 3 C, dotted area).

"*Penaeus*" *meyeri* OPPEL (= MÜNSTER's *Antrimpos senidens*, *Koelga quadridens*, *K. dubia*, and *K. tridens*, considered as nomina dubia by OPPEL (1862)): lateral lobe strongly curved, increasing in width and terminating in a rather thin, presumably flexible, dorsally broadened, spatula- to shovel-shaped part (Fig. 3 D). This petasma shows a clearly diverging shape compared with the other species. Though a penaeid, the species is probably not a member of the genus *Antrimpos*.

5. References

BAIER, F. I. (1757): Ioannis Iacobi Baieri Monumenta Rerum Petrificarum Praecipua Oryctographiae Noricae Supplementi Loco Iungenda. Interprete Filio Ferdinando Iacobo Baiero; 20 pp.; Nürnberg (Lichtensteger).

BALSS, H. (1922): Studien an fossilen Decapoden. – Paläontologische Zeitschrift, **5**: 123–147.

BATE, C. S. (1888): Report on the Crustacea Macrura collected by H. M. S. Challenger during the years 1873–76. Scientific Results of the Exploring Voyage of H. M. S. Challenger, 1873–76, **24**: 1–942.

BAUER, R. T. (1991): Sperm Transfer and Storage Structures in Penaeoid Shrimps: A Functional and Phylogenetic Perspective. – In: BAUER, R. T. & MARTIN, J. W. (eds.): Crustacean Sexual Biology, pp. 183–207; New York (Columbia University Press).

DALL, W., HILL, B. J., ROTHLISBERG, P. C. & STAPLES, D. J. (1990): The Biology of the Penaeidae. – Advances in Marine Biology, **27**: 489 pp.

DIETL, G., DIETL, O., SCHWEIGERT, G. & HUGGER, R. (2000): Der Nusplinger Plattenkalk (Weißer Jura ζ) – Grabungskampagne 1999. – Jahreshefte der Gesellschaft für Naturkunde in Württemberg, **156**: 5–26.

DIETL, G., SCHWEIGERT, G., FRANZ, M. & GEYER, M. (1998): Profile des Nusplinger Plattenkalks (Oberjura, Schwäbische Alb). – Stuttgarter Beiträge zur Naturkunde, Serie B, **265**: 37 pp.

ENGEL, T. (1908): Geognostischer Wegweiser durch Württemberg. 3rd edition. XXX + 645 pp.; Stuttgart (Schweizerbart).

FABRICIUS, J. C. (1798): Supplementum Entomologiae Systematicae. 572 pp.; Hafniae (Proft & Storch).

FRAAS, E. (1910): Der Petrefaktensammler. 239 pp.; Stuttgart (K. G. Lutz).

FRAAS, O. (1855): Beiträge zum obersten weissen Jura in Schwaben. – Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, **11**: 77–107.

GLAESSNER, M. F. (1929): Fossilium Catalogus, I. Animalia, 41, Crustacea decapoda. 464 pp.; Berlin (Junk).

KLAUS, S., SCHUBART, C. D. & BRANDIS, D. (2006): Phylogeny, biogeography and a new taxonomy for the Gecarcinucoidea RATHBUN, 1904 (Decapoda: Brachyura). – Organisms Diversity & Evolution, **6**(3): 199–217.

MILNE EDWARDS, H. (1837): Histoire Naturelle des Crustacés, comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux, **2**: 1–532; Paris (Robert).

MÜNSTER, G. GRAF ZU (1839): Decapoda Macroura. Abbildung und Beschreibung der fossilen langschwänzigen Krebse in den Kalkschiefern von Bayern. – Beiträge zur Petrefactenkunde, **2**: 1–88.

OPPEL, A. (1862): Über jurassische Crustaceen. – Palaeontologische Mittheilungen aus dem Museum des Koeniglich Bayerischen Staates, **1**: 1–120.

PÉREZ FARFANTE, I. & KENSLEY, B. (1997): Penaeoid and Sergestoid Shrimps and Prawns of the World. Keys and Diagnoses for the Families and Genera. – Mémoires du Muséum National d'Histoire Naturelle, **175**: 132 pp.

POLZ, H. (2002): Das Petasma – Geschlechts- und Art-Bestimmungsmerkmal penaeider Garnelen. – Archaeopteryx, **20**: 39–50.

POLZ, H. (2003): Petasmata der Gattung *Aeger* MÜNSTER, 1839 (Crustacea: Decapoda: Penaeoidea) und ihre phylogenetische Bedeutung. – Archaeopteryx, **21**: 13–18.

QUENSTEDT, F. A. (1852): Handbuch der Petrefaktenkunde. Krebse. Crustacea. pp. 259–306; Tübingen (H. Laupp).

QUENSTEDT. F. A. (1856–1857): Der Jura. 842 pp.; Tübingen (H. Laupp).

SCHWEIGERT, G. (2001): Eine neue Art der Gattung *Antrimpos* MÜNSTER (Crustacea, Decapoda, Penaeidae) aus dem Nusplinger Plattenkalk (Oberjura, Ober-Kimmeridgium, SW-Deutschland). – Stuttgarter Beiträge zur Naturkunde, Serie B, **307**: 33 pp.

Schweigert, G. & Garassino, A. (2004): New genera and species of shrimps (Crustacea: Decapoda: Dendrobranchiata, Caridea) from the Upper Jurassic lithographic limestones of S Germany. – Stuttgarter Beiträge zur Naturkunde, Serie B, **350**: 33 pp.

Straelen, V. van (1925): Contribution à l'étude des crustacés decapodes de la période jurassique. – Mémoires de l'Académie Royale de Belgique, 2ème série, **7**: 1–462.

Walch, J. E. I. (1773): Die Naturgeschichte der Versteinerungen zur Erläuterung der Knorrischen Sammlung von Merkwürdigkeiten der Natur. Vierter Theil; 128 pp.; Nürnberg (Felßecker).

Walther, J. (1904): Die Fauna der Solnhofener Plattenkalke. Bionomisch betrachtet. – Denkschriften der Medizinisch-Naturwissenschaftlichen Gesellschaft zu Jena, **11** (E. Haeckel Festschrift): 133–214.

Woods, H. (1925): A monograph of the fossil macrurous Crustacea of England. – Palaeontographical Society Monographs: 40 pp.

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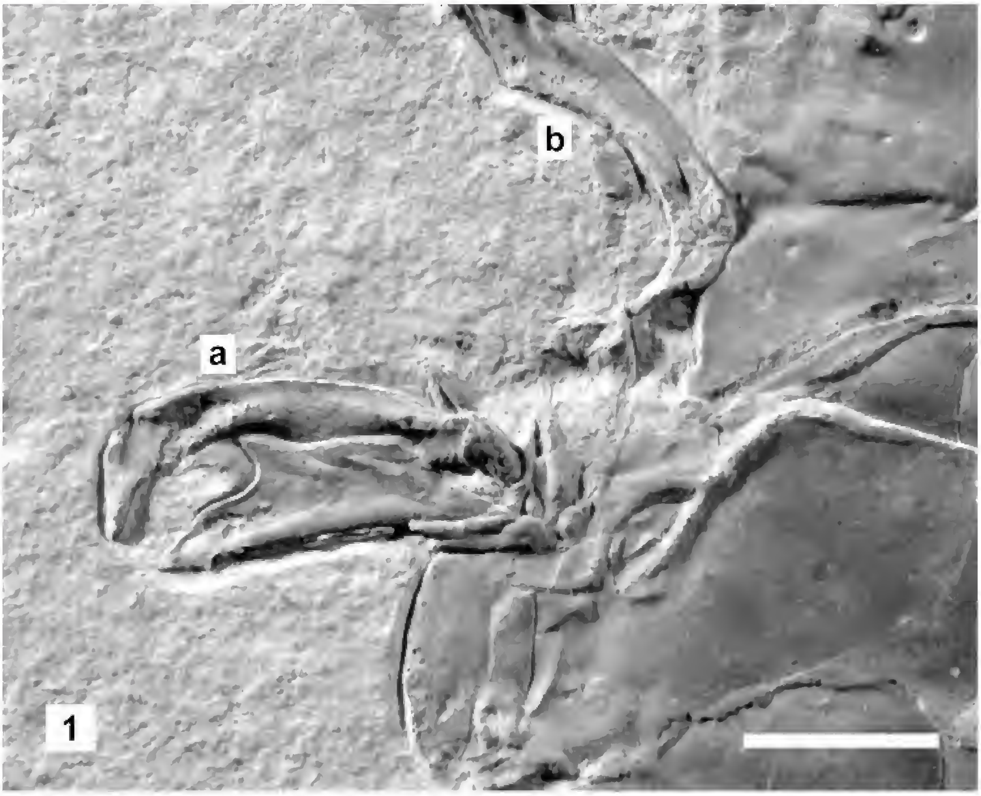
Plate 1

Antrimpos undenarius Schweigert. Nusplingen Lithographic Limestone, Nusplingen quarry, bed L, Upper Kimmeridgian, Beckeri Zone, Ulmense Subzone. SMNS 66122. – Scale bars 1 mm.

Fig. 1. Petasma (a) and disintegrated lateral lobe of second half of petasma (b).

Fig. 2. As Fig.1, in ultraviolet illumination.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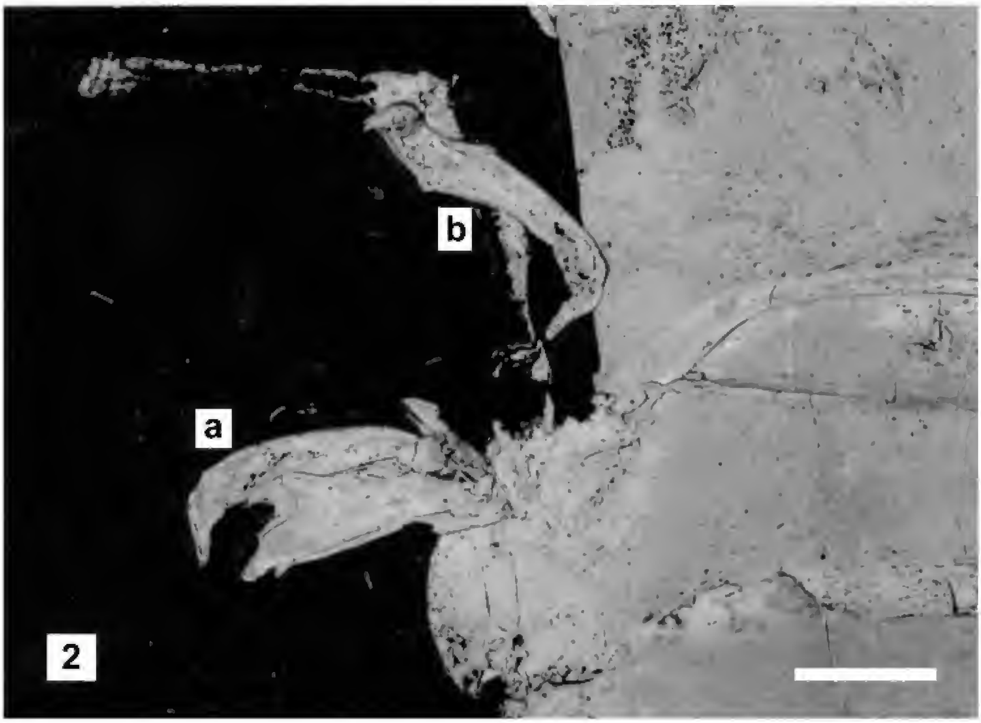
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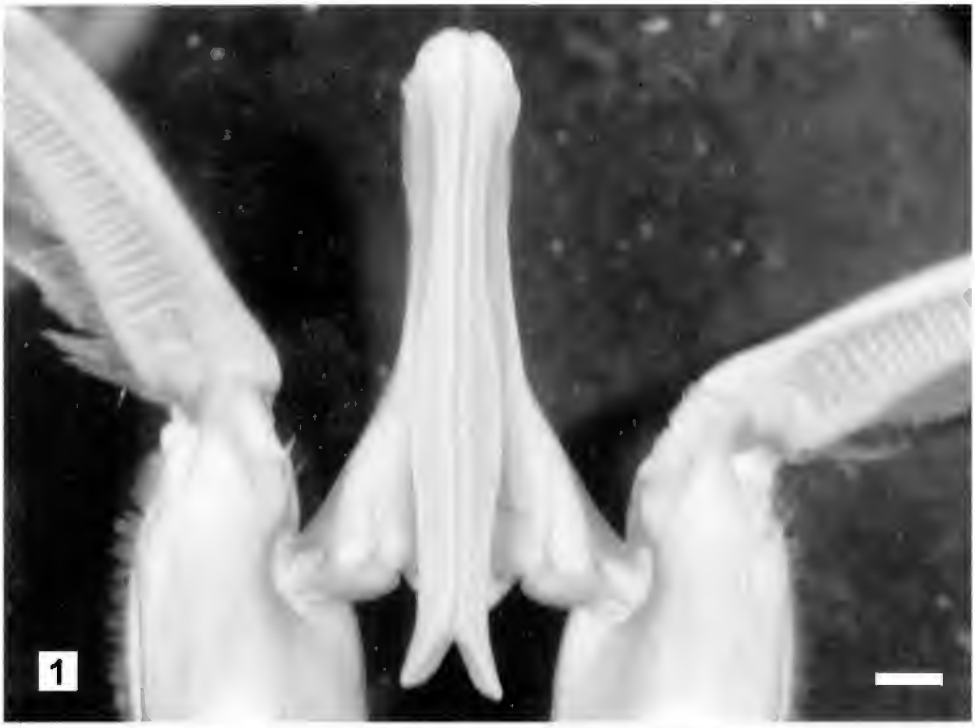
Plate 2

Petasmata of living Penaeidae; author's collection. – Scale bars 1 mm.

Fig. 1. *Marsupenaeus japonicus* (Bate); petasma (= coupled endopods) between pleopods 1, dorsal view; coll. no. 06072302.

Fig. 2. *Marsupenaeus japonicus* (Bate); petasma anteriorly directed, distally extending to the bases of pereiopods 4 (P4); coll. no. 06072301.

Fig. 3. Isolated sides of petasmata. **a:** *Marsupenaeus japonicus* (Bate); right half (= right endopod), ventrolateral view; median lobe on the right; coll. no. 06072303. **b:** *Fenneropenaeus indicus* (H. Milne Edwards); left half (= left endopod), ventral view; lateral lobe and ventral costa on the right; coll. no. 06080101.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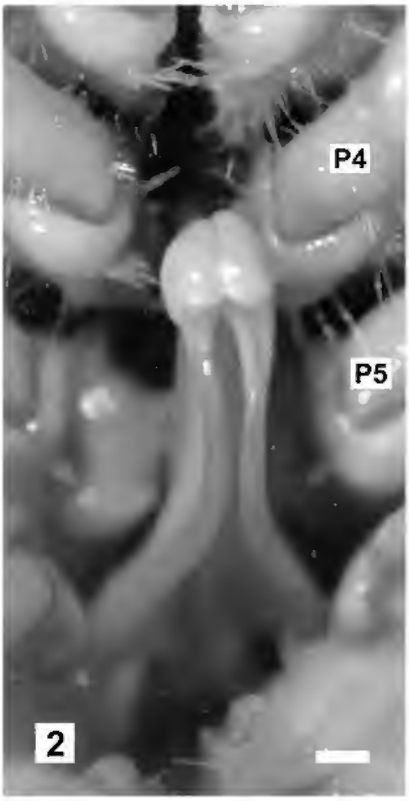
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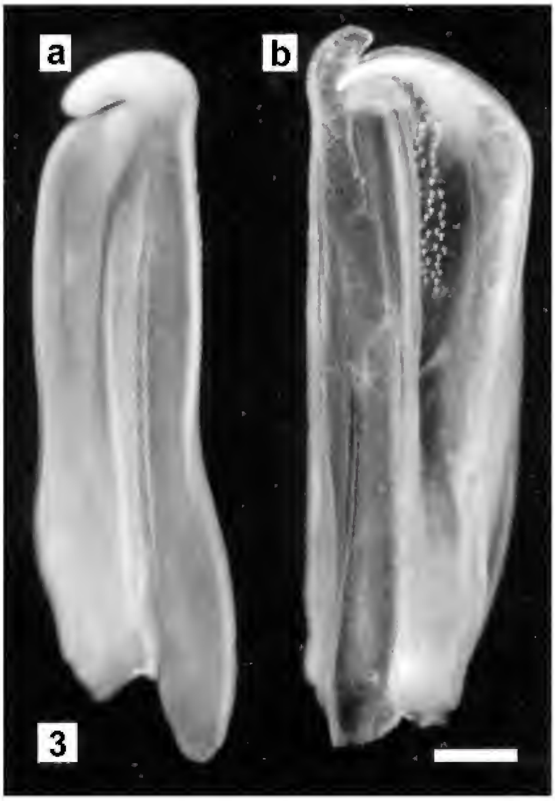
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Jurassische Gastropoden aus der Betakalkbank (oberes Sinemurium, obere Obtusum-Zone) Südwestdeutschlands

Jurassic Gastropods from the Betakalkbank (Upper Sinemurian, Upper Obtusum Zone) of southwestern Germany

Joachim Gründel

Abstract

17 gastropod species are described from the Betakalkbank (Upper Sinemurian, Upper Obtusum Zone) in Baden-Württemberg (southwestern Germany), 10 of them in open nomenclature. New are *Anticonulus jaegeri* n. sp., *Trypanotrochus*? *broesamleni* n. sp., *Ataphrus naricopsiformis* n. sp., *Lewisiella ventrocostata* n. sp., *Katosira basistriata* n. sp., and *Protorcula*? *quadricostata* n. sp., and the genus *Costataphrus* n. gen. with the type species *Turbo admirandus* Tate, 1870. The described fauna has the greatest number of species and the best preservation known to date from the Betakalkbank in southwestern Germany.
Keywords: Gastropoda, taxonomy, Upper Sinemurian (Lower Jurassic), southwestern Germany.

Zusammenfassung

Aus der Betakalkbank (oberes Sinemurium, obere Obtusum-Zone) von Baden-Württemberg (Südwestdeutschland) werden 17 Gastropoden-Arten beschrieben, davon 10 in offener Nomenklatur. Neu sind *Anticonulus jaegeri* n. sp., *Trypanotrochus*? *broesamleni* n. sp., *Ataphrus naricopsiformis* n. sp., *Lewisiella ventrocostata* n. sp., *Katosira basistriata* n. sp. und *Protorcula*? *quadricostata* sowie die Gattung *Costataphrus* n. gen. mit der Typusart *Turbo admirandus* Tate, 1870. Die Fauna ist die mit Abstand artenreichste und am besten erhaltene aus der Betakalkbank des südwestlichen Deutschlands.

1. Einleitung mit Bemerkungen zur Betakalkbank

Gut erhaltene Gastropoden aus dem tieferen unteren Jura Süddeutschlands sind selten. Zusammenfassende Darstellungen gaben Brösamlen (1909) und Hägele (1997). Gründel (2003) lieferte eine Neubearbeitung der aus dem oberen Hettangium bis unteren Sinemurium bekannten Gastropoden des Gebietes.

Gastropodenfunde aus der fossilreichen Betakalkbank sind selten. Ihre Erhaltung ist oft nicht gut bzw. sie sind aus den splittrigen Kalken nicht zu gewinnen. Nach Umfang und Erhaltung einmalig ist die von Dr. M. JÄGER (Dotternhausen) 1995 geborgene Fauna. Fundstelle ist der tiefste Teil einer Senke im Verlauf der B 27 zwischen Hechingen und Bisingen (Aushub eines Teiches im Mittelstreifen der B 27, ein temporärer Aufschluß). Zutage kamen Knollen des sehr harten, dunkelgrauen Kalkes der Betakalkbank, versehen mit einer braunen Verwitterungsrinde. Aus dieser weichen Rinde konnten die Gastropoden gewonnen werden. Ihre Erhaltung schwankt von mäßig bis sehr gut. Größere Exemplare liegen meist nur in Bruchstücken vor, viele Arten zudem nur mit einem oder wenigen Exemplaren. Das erklärt die häufige Anwendung der offenen Nomenklatur. Ein erneuter Besuch der Fundstelle zusammen mit dem Verfasser lieferte keine neuen Funde.

Stratigraphisch ist die Betakalkbank in die obere Obtusum-Zone des oberen Sinemuriums zu stellen (u.a. BRANDT 1985, HOFFMANN 1964, SÖLL 1956, URLICHS 1977). Es handelt sich um eine Bank dunkelgrauen bis blaugrauen harten, splittrigen Kalkes. Sie führt aus Tonschlamm entstandene „Gerölle". Im Liegenden wird sie meist von einer Lage knolliger Kalkkonkretionen begleitet. Diese Knollen sind weitgehend fossilfrei, während aus der Kalkbank eine arten- und individuenreiche Fauna bekannt ist. Nach QUENSTEDT (1856–57) und nach Angaben von Herrn JÄGER sind bekannt Serpuliden, Bivalven (Gryphaeen), Gastropoden, Ammoniten, Belemniten, Echinodermen (Isocriniden). Die Ammoniten wurden letztmalig von URLICHS (1977) bearbeitet.

Spezielle Untersuchungen zu den Bildungsbedingungen der Betakalkbank fehlen. Nach BRANDT (1985) sind die Konkretionen unter der Betakalkbank frühdiagenetische Bildungen, entstanden in geringer Tiefe. Erosive Prozesse im Bereich der Bank werden durch angebohrte und zerbrochene Konkretionen, Auftreten toniger Einschlüsse und sekundär eingebettete Gryphaeen angezeigt. Die Betakalkbank wurde (nach BRANDT 1985) wahrscheinlich in flachem Wasser, aber unterhalb der normalen Wellenbasis abgelagert. Nach oben geht die Kalkbank über kalkige Mergel fließend in Tone über, was eine allmähliche Vertiefung des Ablagerungsraumes anzeigt.

Dank

Herrn Dr. M. JÄGER (Dotternhausen) hat Verfasser für die Überlassung dieser interessanten, einmaligen Fauna ganz herzlich zu danken. Dr. G. DIETL (Stuttgart) und Dr. H. SCHULZ (Tübingen) machten dem Autor dankenswerter Weise die wertvollen einschlägigen Originale von QUENSTEDT und BRÖSAMLEN zugänglich. Viele Fotos fertigte Frau N. WITTEK (Berlin) an, wofür ihr gedankt sei. Den Herren Dr. R. BÖTTCHER (Stuttgart), Dr. S. KIEL (Leeds) und Dr. A. NÜTZEL (München) hat Verfasser für kritische Durchsicht des Manuskriptes zu danken. Für die gewährte Nutzung der Einrichtungen des Institus für Geologische Wissenschaften, Fachbereich Paläontologie, der Freien Universität Berlin ist Verfasser Herrn Prof. H. KEUPP zu Dank verpflichtet.

2. Beschreibung

Die Holo- und abgebildeten Paratypen sowie alle sonstigen abgebildeten Exemplare werden im Staatlichen Museum für Naturkunde Stuttgart hinterlegt (SMNS 66774–66800), das übrige Belegmaterial geht an Herrn Dr. JAEGER zurück.

Unterklasse Archaeogastropoda THIELE, 1925
Ordnung Vetigastropoda SALVINI-PLAWÉN, 1980
Überfamilie Pleurotomarioidea SWAINSON, 1840
Familie Eotomariidae WENZ, 1938
Unterfamilie Ptychomphalinae WENZ, 1938

Gattung *Ptychomphalus* AGASSIZ, 1837

Typusart: *Helicina expansa* SOWERBY, 1821; Lias; England.

Ptychomphalus sp.
Taf. 1, Fig. 1–2

Material: 14 juvenile bzw. bruchstückhaft erhaltene ältere Exemplare (SMNS 66774, 66775 sowie Sammlung JÄGER).

Beschreibung. – Das größte (unvollständige) Exemplar ist 15 mm breit. Das Gehäuse ist bikonvex. Die Spira ist niedriger als die stark konvexe Basis. Die Windungen grenzen ohne Absatz aneinander. Die letzte Windung verdeckt die vorangegangene bis zur oberen Kante des Schlitzbandes. Die Nähte sind kaum eingetieft. Die größte Breite des Gehäuses wird von der abapikalen Begrenzung des Schlitzbandes oder vom Schalenbereich etwas abapikal von dieser gebildet. Eine Wulst unter der apikalen Naht fehlt frühontogenetisch, ist spätontogenetisch aber sehr deutlich ausgebildet. An einigen Exemplaren ist auf der Wulst eine schwache Höckerbildung erkennbar. Der Schalenbereich zwischen Wulst und abapikaler Naht wird konkav. Die ganze Schalenoberfläche (einschließlich dem Schlitzband) ist mit zahlreichen Spiralfurchen bedeckt. Diese sind auf der Basis deutlich weitständiger als apikal vom Schlitzband. Das Basiszentrum wird von einem breitflächigen Callus verdeckt.

Bemerkungen. – Für eine Benennung ist die Art zu fragmentarisch erhalten.

Beziehungen. – Von der ähnlichen *Ptychomphalus theodorii* (SCHRÜFER, 1861)? sensu GRÜNDEL 1999 unterscheidet sich die Art durch die kräftigere subsuturale Wulst auf späteren Windungen und den deutlich konkaven Umriss zwischen Wulst und Oberkante des Schlitzbandes. *Ptychompahlus theodorii* (SCHRÜFER, 1861) und *P. morieri* EUDES-DESLONGHAMPS, 1866 haben außerdem nach der Originalbeschreibung keine Spiralskulptur (erhaltungsbedingt?, siehe KUHN 1936).

Überfamilie Trochoidea RAFINESQUE, 1815
Familie Trochidae RAFINESQUE, 1815

Bemerkungen. – Die nachfolgend beschriebenen Arten der Gattungen *Anticonulus* und *Trypanotrochus* stellte COX (in KNIGHT et al. 1960) zu den Trochidae, Unterfamilie Proconulinae n. subfam. *Proconulus* COSSMANN, 1918 hat, basierend auf der Typusart, einen anderen Inhalt, als COX (in KNIGHT et al. 1960) dieser Gattung gab (basierend wohl auf der dort abgebildeten *Trochus raulineus* BUVIGNIER, 1852, die weder zu *Proconulus* noch zu den Proconulidae gehört). GRÜNDEL (2000) hat daher die Proconulidae neu definiert. *Anticonulus* und *Trypanotrochus* werden hier provisorisch zu den Trochidae gestellt.

Gattung *Anticonulus* COSSMANN, 1918

Typusart: *Trochus mariae* D'ORBIGNY, 1853; Pliensbachium; Pariser Becken.

Anticonulus jaegeri n. sp.

Taf. 2, Fig. 1

Holotypus: Das auf Taf. 2, Fig. 1 abgebildete Exemplar (SMNS 66778).
Paratypen: 3 Gehäuse bzw. Bruchstücke (Sammlung JÄGER).
Locus typicus: Mittelstreifen der B 27 in einer Senke zwischen Bisingen und Hechingen (Baden-Württemberg).
Stratum typicum: Betakalkbank, obere Obtusum-Zone, oberes Sinemurium.
Derivatio nominis: Zu Ehren des Sammlers der Fauna, Herrn Dr. M. JÄGER, Dotternhausen (Süddeutschland).

Diagnose. – Gehäuse breit konisch, Windungsflanken konkav; die Kante zur Basis liegt in der Sutur; Anwachslinien auf den Windungsflanken deutlich parasigmoidal, in der abapikalen Windungshälfte rippenartig verstärkt; Basis mit Spiralfurchen.

Diagnosis. – Shell broadly conical; flanks of the whorls concave; the edge to the base forms the sutur; growth lines on the flanks distinctly parasigmoidal and strengthened to axial ribs in the lower part of the flanks; base with spiral furrows.

Beschreibung. – Das hoch trochospirale Gehäuse hat einen abgestumpften Apex (die beiden ersten Windungen sind fast planspiral aufgerollt). Die nur langsam an Höhe zunehmenden Windungen sind sehr breit im Verhältnis zu ihrer Höhe. Die Windungsflanken sind schwach konkav. Auf ihnen verlaufen parasigmoidal und stark prosoclin axiale Skulpturelemente. Im apikalen Windungsteil sind sie als betonte Anwachslinien ausgebildet, im abapikalen Teil als schmale Axialrippen. Die kaum konvexe Basis ist durch eine schmal gerundete Kante abgesetzt. Sie ist mit Spiralfurchen bedeckt, die durch Bereiche wechselnder Breite getrennt werden. Zahlreiche schwache Axialrippen verlaufen prosoclin und opisthocyrt. Der Nabel ist eng, aber deutlich. Die niedrige Mündung ist rhombenförmig.

Beziehungen. – Die Merkmalskombination von breitem Gehäuse, konkaven Flanken, parasigmoidalen und im abapikalen Teil der Flanken zu Axialrippen verstärkten Anwachslinien und Spiralfurchen auf der Basis unterscheidet die Art von ähnlichen Arten der Gattung (z. B. *Trochus basistriatus* BRÖSAMLEN, 1909).

Gattung *Trypanotrochus* COSSMANN, 1918

Typusart: *Trochus normanianus* D'ORBIGNY, 1853 (= *Trochus gea* D'ORBIGNY, 1853 nach FISCHER & WEBER 1997).

Bemerkungen. – Die Typusart der Gattung hat einen deutlichen Umbilikus.

Dieser fehlt der nachfolgend beschriebenen Art. Sie wird daher nur mit Vorbehalt hierher gestellt.

Trypanotrochus? *broesamleni* n. sp.
Taf. 2, Fig. 2

Holotypus: Das auf Taf. 2, Fig. 2 abgebildete Exemplar (SMNS 66779).
Paratypen: 8 Gehäuse und Bruchstücke (Sammlung Jäger).
Locus typicus: Mittelstreifen der B 27 in einer Senke zwischen Bisingen und Hechingen (Baden-Württemberg).
Stratum typicum: Betakalkbank, obere Obtusum-Zone, oberes Sinemurium.
Derivatio nominis: Im Andenken an R. Brösamlen, der die südwestdeutschen Juragastropoden in vorbildlicher Weise beschrieben hat.

Diagnose. – Gehäuse schlank mit schwach konkaven Windungsflanken; auf den Flanken wechseln starke und schwache Spiralrippen; Axialrippen zahlreich, aber schwach (fast nur verstärkte Anwachslinien); Kiel mit zahlreichen Höckern; Basis mit 7–8 gleich starken Spiralrippen.

Diagnosis. – Shell slender; flanks of the whorls weakly concave; strong and weak spiral ribs alternate on the flanks; axial ribs numerous but weak (similar strengthened growth lines); keel with numerous nodes; base with 7–8 spiral ribs equal in strength.

Beschreibung. – Das größte (unvollständige) Exemplar ist ca. 10 mm hoch. Das verhältnismäßig schlanke Gehäuse hat eine hohe Spira und gerade bis schwach konkave Windungsflanken. Die Gehäusespitze ist nicht vollständig bzw. schlecht erhalten. Die erste erkennbare Skulptur besteht aus 3 etwa gleich starken Spiralrippen. Die abapikale kielt den Windungsumriss. Eine sekundäre Spiralrippe erscheint bald zwischen apikaler und mittlerer primärer Spiralrippe. Je eine weitere wird etwas später zwischen apikaler Naht und apikaler primärer Spiralrippe sowie zwischen letzterer und der abapikalwärts folgenden Spiralrippe angelegt. Zahlreiche schwache prosocline Axialrippen (fast nur verstärkte Anwachslinien) höckern die Spiralrippen. Der dicht oberhalb der abapikalen Naht gelegene Kiel wird verstärkt. Die Höcker auf ihm sind nicht wie sonst gerundet, sondern in Richtung der Axialrippen verlängert. Die wenig konvexe Basis ist mit 7–8 (einschließlich der Grenzspiralrippe) etwa gleich starken Spiralrippen ganz bedeckt. Diese werden von sehr zahlreichen prosoclinen und opisthocyrten Axialrippen schwach gehöckert. Die Mündung ist etwa ebenso breit wie hoch. Die Außenlippe ist im Kielbereich deutlich gewinkelt.

Bemerkungen. – Brösamlen (1909) beschrieb aus der Betakalkbank die Art *Trochus percarinatus* n. sp. Ihm lag nur ein Exemplar vor. Der Verfasser konnte es im Staatlichen Museum für Naturkunde Stuttgart sehen. Es hat eine der *T.*? *broesamleni* ähnliche Gestalt. Die Gehäusespitze fehlt. Es ist korrodiert mit undeutlich erhaltener Skulptur. Auf der Basis und an der Mündung sind Details nicht erkennbar. Nach Auffassung des Autors ist das Exemplar ungeeignet für die Begründung einer neuen Art, da an ihm wesentliche Merkmale nicht erkennbar sind. *Trochus percarinatus* ist als nomen dubium zu werten.

Gehäusegestalt und Skulptur der *Trypanotrochus*? *broesamleni* entsprechen denen der Typusart von *Trypanotrochus.* Letztere hat jedoch einen deutlichen Umbilikus. *Trypanotrochus*? *broesamleni* wird deshalb mit Vorbehalt zur Gattung *Trypanotrochus* gestellt.

Beziehungen. – Die Unterschiede zur *Gerasimovcyclus triplicatus* (MARTIN, 1862)? siehe bei dieser.

Familie Nododelphinulidae COX in KNIGHT et al., 1960

Gattung *Metriomphalus* COSSMANN, 1915

Typusart: *Turbo davoustii* D'ORBIGNY, 1850; Bajocium; Frankreich.

Metriomphalus? sp., cf. *thetis* (V. MÜNSTER, 1844)

Taf. 1, Fig. 3–4

non 1844 *Trochus thetis* MÜNSTER. – MÜNSTER in GOLDFUSS 1826–1844, S. 54, Taf. 179, Fig. 10a–b.
1887 *Trochus thetis* MÜNST. – WILSON, S. 4, Taf. 5, Fig. 2a–c.
? 1997 *Riselloidea periniana* (D'ORBIGNY, 1853). – FISCHER & WEBER, S. 103, Taf. 21, Fig. 24.

Material: 7 Gehäuse und Bruchstücke (SMNS 66776, 66777 sowie Sammlung JÄGER).

Beschreibung. – Die fragmentarisch überlieferte Art wurde mindestens 10 mm hoch. Die Windungen werden durch eine oberhalb der abapikalen Naht gelegene kräftige Spirale gekielt. Der Bereich apikal vom Kiel ist gegen den Apex geneigt. Der Bereich zwischen Kiel und abapikaler Naht steht etwa senkrecht und ist konkav. Unter der apikalen Naht verläuft eine gehöckerte Spirale. Von ihren Höckern gehen stark prosocline und teilweise etwas opisthocyrte Axialrippen zum Kiel und höckern diesen ebenfalls. Die Höcker des Kiels bilden auf späteren Windungen auf ihrer Vorderseite eine Vertiefung aus. Vom Kiel verlaufen zur oberhalb der Naht sichtbar werdenden Grenzspiralrippe zahlreiche schwache, prosocline Axialrippen und bilden auf letzterer kleine Höcker. Auf späten Windungen wird im Bereich zwischen apikaler Höckerreihe und Kiel ein zweites System schwächerer Axialrippen gebildet, das schräg zu den Hauptrippen verläuft. Die flache Basis ist an der Grenzspiralrippe winklig abgesetzt. Auf ihr verlaufen 4 weitere kräftige Spiralrippen. Sie werden von zahlreichen stark prosoclinen und etwas opisthocyrten Axialrippen gequert, aber nicht gehöckert. Ein deutlicher Nabel ist ausgebildet. Die Ausbildung der Mündung ist unbekannt.

Bemerkungen. – Der wahrscheinlich identischen von WILSON (1887) als *Trochus thetis* MÜNSTER aus England beschriebenen Form fehlt die Höckerung der Grenzspiralrippe. Sie und die hier beschriebene Art sind nicht identisch mit der von V. MÜNSTER 1844 (in GOLDFUSS 1826–1844) beschriebenen *Trochus thetis*. Letztere hat u. a. ein breiteres Gehäuse und die Axialrippen sind zahlreicher, es fehlen die Vertiefungen auf den Höckern und die schräg verlaufenden schwächeren Axialrippen, die Grenzspiralrippe ist schwächer gehöckert (siehe auch BRÖSAMLEN 1909: 207, Taf. 17, Fig. 16a–d). Recht ähnlich wird *Riselloidea periniana* (D'ORBIGNY, 1853) (siehe FISCHER & WEBER 1997). Sie ist aus dem oberen Pliensbachium bekannt und hat ein schlankeres Gehäuse. Da auch diese Art nur unvollkommen bekannt ist, ist ein näherer Vergleich mit der vorliegenden nicht möglich.

Familie Eucyclidae KOKEN, 1896

Gattung *Eucycloscala* COSSMANN, 1895

Typusart: *Trochus binodosus* v. MÜNSTER, 1841; obere Trias; italienische Alpen.

Eucycloscala sp., cf. *brunhuberi* (SCHNITTMANN, 1966)

Taf. 2, Fig. 3

? 1966 *Trochus brunhuberi* n. sp. – SCHNITTMANN, S. 86, Abb. 22.

Material: 3 Exemplare (SMNS 66780 und Sammlung JÄGER).

Beschreibung. – Es liegen wohl nur Juvenile vor. Auf den Protoconch (die Grenze zum Teleoconch ist nicht deutlich) folgt ca. eine gerundete, glatte Windung. Zögernd setzen dann 2 Spiralrippen sowie prosocline Axialrippen ein. Je eine zusätzliche Spiralrippe erscheint bald unter der apikalen Naht sowie zwischen den beiden primären Spiralrippen. Nur auf den ersten Windungen sind die beiden primären Spiralrippen kräftiger als die anderen und winkeln den Windungsumriss etwas. Bald sind alle Spiralrippen etwa gleich stark und die Flanken werden mehr oder weniger gerade sowie gegen den Apex geneigt. Die abapikale Spiralrippe bildet die größte Gehäusebreite. Eine weitere Spiralrippe wird (immer?) zwischen den beiden apikal gelegenen Spiralrippen gebildet. Zahlreiche gerade, prosocline Axialrippen höckern die Spiralrippen. Auf der letzten Windung des abgebildeten Exemplars hat die apikale Spiralrippe 26 Höcker, die am weitesten abapikal gelegene knapp 50. Die stark konvexe Basis ist nicht abgesetzt. Sie ist ganz mit 9–10 (einschließlich der Grenzspiralrippe) etwa gleich starken Spiralrippen bedeckt. Diese werden von zahlreichen geraden und prosoclinen, verstärkten Anwachslinien gequert. Ein Nabel fehlt. Die Mündung ist sehr breit oval. Ihr Rand ist im Übergangsbereich Columella/Außenlippe etwas verbreitert.

Bemerkungen. – SCHNITTMANN (1966) bildete seine neue Art völlig unzureichend ab. Aus der recht ausführlichen Beschreibung ergeben sich Ähnlichkeiten zur vorliegenden Art. Da SCHNITTMANN's Art nur wenig jünger ist (unterster Lias? = unteres Carixium) und ebenfalls in Süddeutschland auftritt, wurde die vorbehaltliche Zuordnung vorgenommen.

Beziehungen. – *E. brunhuberi* hat eine weniger stark konvexe Basis mit gehöckerten Spiralrippen, auf den Windungsflanken 5–6 gleichstarke Spiralrippen und ebenso kräftige Axialrippen. Andere ähnliche Arten (z.B. *Trochus carinellaris* BUVIGNIER, 1852, *Turbo nireus* D'ORBIGNY, 1852, *Turbo piatoni* DUMORTIER, 1867) haben neben anderen Unterschieden deutlich stärker konvexe Basen.

Gattung *Gerasimovcyclus* GRÜNDEL, 2005

Typusart: *Fusus clathratus* LAHUSEN, 1883; Oxfordium; Russische Plattform.

Gerasimovcyclus triplicatus (MARTIN, 1862)?
Taf. 3, Fig. 1

Material: Ein juveniles Gehäuse (SMNS 66781).

Beschreibung. – Das Gehäuse ist breit konisch. Die Windungen werden durch eine dicht oberhalb der abapikalen Naht gelegene Spiralrippe gekielt. Auf den ersten schlecht erhaltenen Windungen kanten möglicherweise zwei Spiralrippen den Windungsumriss (nicht sicher erkennbar). Dann sind drei kräftige Spiralrippen erkennbar (den Kiel eingeschlossen). Etwas später wird zwischen ihnen sowie zwischen Kiel und abapikaler Naht je eine schwächer bleibende Spiralrippe gebildet. Zahlreiche prosocline und opisthocyrte Axialrippen höckern die Spiralrippen. Die Axialrippen bleiben schwach. Ontogenetisch steigt die Zahl der Höcker auf dem Kiel. Sie werden auch kleiner als die Höcker auf den beiden anderen primären Spiralrippen. Die deutlich konvexe Basis ist an der Grenzspiralrippe nicht abgesetzt. Sie ist mit zahlreichen Spiralrippen bedeckt, wobei jeweils eine kräftige mit einer schwächeren abwechselt. Viele schwache Axialrippen höckern sie etwas. Die Mündung ist rundlich. Die Außenlippe ist im Bereich des Kiels schwach gewinkelt. Ein abapikaler Kanal ist ausgebildet.

Bemerkungen. – Die von MARTIN (1862) beschriebene Art stammt aus etwa gleichalten Schichten. Sie hat die gleiche Skulptur (u.a. die feine Krenulierung des Kiels). Die Ausbildung der Mündung ist unbekannt, die Gleichsetzung beider daher nicht sicher.

Beziehungen. – *Trypanotrochus*? *broesamleni* n.sp. ist schlanker, die Windungsflanken sind schwach konkav, es werden weniger sekundäre Spiralrippen und in anderer Reihenfolge gebildet, die Basis ist flacher und es fehlt auf ihr der Wechsel stärkerer und schwächerer Spiralrippen, die Mündung ist im Bereich des Kiels deutlicher gewinkelt und es fehlt der abapikale Kanal. *Eucycloscala* sp., cf. *brunhuberi* (SCHNITTMANN, 1966) hat keinen abapikalen Mündungskanal, die Höckerung des Kiels ist gröber, auf den Windungsflanken sind mehr Spiralrippen ausgebildet und auf der Basis fehlt der Wechsel stärkerer und schwächerer Spiralrippen.

Familie Colloniidae COSSMANN in COSSMANN & PEYROT, 1917
Unterfamilie Ataphrinae COSSMANN, 1918

Gattung *Ataphrus* GABB, 1869

Typusart: *Ataphrus crassus* GABB, 1869; Oberkreide; Kalifornien (USA).

Ataphrus naricopsiformis n. sp.

Taf. 5, Fig. 2–4

? 1997 *Ataphrus (Endianaulax) euomphalus* (QUENSTEDT, 1858). – HÄGELE, S. 54, Abb.

Holotypus: Das auf Taf. 5, Fig. 3 abgebildete Exemplar (SMNS 66795).

Paratypen: 39 Gehäuse, Juvenile und Bruchstücke (SMNS 66794, 66796 sowie Sammlung JÄGER).

Locus typicus: Mittelstreifen der B 27 in einer Senke zwischen Bisingen und Hechingen (Baden-Württemberg).

Stratum typicum: Betakalkbank, obere Obtusum-Zone, oberes Sinemurium.

Derivatio nominis: Nach der gestaltlichen Ähnlichkeit mit *Naricopsina*-Arten.

Diagnose. – Gehäuseform ähnlich der von *Naricopsina*-Arten; Spira niedrig, aber deutlich; Windungen gleichmäßig konvex; Mündungsöffnung rund; der deutliche Callus am unteren Ende der Innenlippe endet apikal abrupt; ein Höcker fehlt.

Diagnosis. – Shell shape similar to *Naricopsina* species; spira low but distinct; whorls regularly convex; opening of aperture round; callus on the lower part of the inner lip with a broad adapical end; no tubercle developed.

Beschreibung. – Das größte Exemplar ist 10 mm breit. Das Gehäuse hat naticiden Habitus. Die Spira ist deutlich. Die ersten Windungen sind fast planspiral. Eine Skulptur (außer Anwachslinien) fehlt. Der Protoconch hat einen Durchmesser von 0,24 mm. Die Teleoconchwindungen sind stark konvex mit deutlichen Nähten. Die Basis hat einen engen, tiefen Nabel. Die Anwachslinien rauen die Schalenoberfläche auf. Sie verlaufen gerade und prosoclin. Nur kurz unter der apikalen Naht versteilen sie. An älteren Exemplaren sind in der Umgebung des Nabels schwache radiale Wülste ausgebildet. Die Mündung ist fast rund mit apikalem Ausguss. Die columellare Innenlippe bildet einen breiten, halbmondförmigen Callus, der den Nabel nicht verdeckt. Apikal endet er ziemlich abrupt, abapikal verschmälert er sich allmählich in die Außenlippe.

Bemerkungen. – Die Gehäuseform erinnert mehr an *Naricopsina* als an *Ataphrus*. Die Gestaltung des Callus belegt die Zugehörigkeit zu den Ataphrinae. Innerhalb dieser Unterfamilie wird *Ataphrus* am ähnlichsten. *Endianaulax* COSSMANN, 1902 (in CHARTRON & COSSMANN 1902), zu der HÄGELE (1997) die Art stellte, hat keinen Umbilicus und keine Furche auf dem columellaren Callus.

QUENSTEDT (1856, 1881–84) und BRÖSAMLEN (1909) bildeten als *Turbo* bzw. *Teinostoma euomphalus* QUENSTEDT, 1856 aus der Betakalkbank eine ähnliche, aber sehr niedrig trochospirale Form ab. Das Material zu QUENSTEDT 1881–84 (vom Verfasser gesehen) besteht aus 3 schlecht erhaltenen Exemplaren sowie einem besser erhaltenen Exemplar (alle Tübingen). Letzteres ist sowohl das Original zu QUENSTEDT 1856 (Taf. 19, Fig. 38) als auch zu QUENSTEDT 1881–84 (Taf. 201, Fig. 119) und zu BRÖSAMLEN 1909 (Taf. 19, Fig. 35). Es ist eine sehr niedrige, breite Form. Verdrückungen sind nicht erkennbar. Die Windungen nehmen sehr schnell an Breite zu. Den Übergang von der Flanke zu Basis bildet eine gerundete Kante. Die Mündung ist bei allen schlecht erhalten. Ein Callus ist an keinem erkennbar, dafür ist der Umbilicus groß. Obwohl die Exemplare aus der Betakalkbank stammen, ist ihre Identität mit der vorliegenden Art sehr unwahrscheinlich. Die Unterschiede sind auch bei Berücksichtigung der Unsicherheiten infolge der Erhaltung zu groß. HÄGELE's Zeichnung (1997, auf Seite 54) zeigt eine Form mit etwas höherer Spira als bei der

QUENSTEDT'schen Form. Er beschrieb auch als erster die Ausbildung des Callus (entsprechend der vorliegenden Art), doch seine Zeichnung zeigt einen einfacheren Bau.

Beziehungen. – Die Gehäuseform (ähnlich der Gestalt der Arten der Gattung *Naricopsina*) in Verbindung mit der niedrigen Spira und den gleichmäßig gerundeten Windungen sowie dem breiten, apikal abrupt endenden Callus ohne Höcker unterscheiden *Ataphrus naricopsiformis* n. sp. von den anderen *Ataphrus*-Arten.

Gattung *Lewisiella* STOLICZKA, 1868

Typusart: *Pitonnellus conicus* D'ORBIGNY, 1853; Pliensbachium; Frankreich.

Lewisiella ventrocostata n. sp.
Taf. 3, Fig. 2–3

Holotypus: Das auf Taf. 3, Fig. 3 abgebildete Exemplar (SMNS 66783).

Paratypen: 11 Gehäuse und Bruchstücke (SMNS 66782 sowie Sammlung JÄGER).

Locus typicus: Mittelstreifen der B 27 in einer Senke zwischen Bisingen und Hechingen (Baden-Württemberg).

Stratum typicum: Betakalkbank, obere Obtusum-Zone, oberes Sinemurium.

Derivatio nominis: Nach der mit Spiralrippen bedeckten Basis.

Diagnose. – Gehäuse breit konisch; Basis mit kräftigem runden Callus, umgeben von einer Grube; Basis ganz bedeckt mit deutlichen Spiralrippen.

Diagnosis. – Shell broadly conical; base with a strong, round callus, surrounded by a groove; base densely covered with distinct spiral ribs.

Beschreibung. – Das breit konische Gehäuse hat konvexe Windungen mit deutlichen Nähten. Der Apex ist abgestumpft, da die ersten Windungen sehr niedrig trochospiral sind. Der Protoconch vom Archaeogastropoda-Typ ist ohne erkennbare Skulptur. Er hat einen Durchmesser von 0,21 mm. Auch die Windungen des Teleoconchs sind skulpturlos. Erkennbar sind nur stark prosocline, gerade Anwachslinien. Die mäßig konvexe Basis ist durch eine stark gerundete Kante gegen die Windungsflanke abgesetzt. Das Zentrum bildet ein kräftiger, knopfförmiger Callus, der von einer tiefen Rinne umgeben wird. Die Außenkante der Rinne bildet eine etwas stärkere Spiralrippe. Die Basis ist mit zahlreichen Spiralrippen bedeckt. Sie sind in der Rinne etwas schwächer. Die Mündung ist fast kreisrund.

Beziehungen. – *Pitonnellus conicus* D'ORBIGNY, 1853 sensu STOLICZKA 1861 (mittlerer Lias) hat Spiralrippen auch auf den Windungsflanken, die Windungen sind gekielt und die die Basisgrube umrundende Spiralrippe ist weiter von der Basismitte entfernt. Die aus dem Pliensbachium Westeuropas von FISCHER & WEBER (1997) neu beschriebene *P. conicus* D'ORBIGNY, 1853 ist skulpturlos. Auch andere Arten der Gattung (z. B. *Pitonnellus sordidus* TATE & BLAKE, 1876, *Turbo valvata* QUENSTEDT, 1856, *Trochus nudus* v. MÜNSTER, 1844) haben keine Spiralskulptur.

Gattung *Costataphrus* n. gen.

Typusart: *Turbo admirandus* TATE, 1870; unteres Pliensbachium; England.

Derivatio nominis: Lat. „costa“ = Rippe, nach der kräftigen Rippenskulptur, in Verbindung mit *Ataphrus*.

Diagnose. – Erste Teleoconchwindungen gekantet bis gekielt, mit breiter Rampe, spätontogenetisch rundet die Kante ab; Skulptur aus zahlreichen kräftigen Axialrippen und (meistens) Spiralrippen bestehend, die Kreuzungsstellen können gehöckert sein; Basis mit Nabel, aber ohne Nabelwulst; columellarer Callus halbmondförmig mit Furche.

Diagnosis. – First teleoconch whorls with edge or keel and a distinct ramp; sculpture consists of numerous, strong axial ribs and usually spiral ribs, their intersections are sometimes nodular; basis with umbilicus but without encircling rib; callus crescent-shaped with a furrow.

Beziehungen. – Gestalt und Ausbildung des Callus belegen enge Beziehungen der neuen Gattung zu *Angulataphrus* Gründel, 2003 und damit zu den Ataphrinae. *Angulataphrus* fehlt die Axialskulptur, der Umbilicus wird von einer gerundeten Rippe bzw. einem Wulst umrundet. *Socconella* Fischer & Weber, 1997 fehlt ein Umbilicus und in der Mündung ist ein „callus columellaire interne“ (Fischer & Weber 1997: 134) (ein Septum?) ausgebildet, weshalb die Autoren ihre Gattung zu den Neritidae/Neritinae stellten. Es fehlt der äußere halbmondförmige columellare Callus, wie er für *Costataphrus* und verwandte Gattungen charakteristisch ist.

Costataphrus admirandus (Tate, 1870)

Taf. 3, Fig. 4; Taf. 4, Fig. 1

1870 *Turbo admirandus* nov. sp. – Tate, S. 403, Taf. 26, Fig. 10.

Material: 3 Gehäuse (SMNS 66784 sowie Sammlung Jäger).

Beschreibung. – Das abgebildete Exemplar ist mit ca. 5 Windungen 3,7 mm hoch und 3,9 mm breit. Das breit trochospirale Gehäuse hat einen abgeflachten Apex (fast planspirale erste Windungen). Der Protoconch lässt keine Skulptur erkennen und hat einen Durchmesser von 0,23 mm. Die Windungen des Teleoconchs sind anfangs gerundet. Ihre Skulptur besteht aus mehreren Spiralrippen und undeutlichen (erhaltungsbedingt?) verstärkten Anwachslinien. Nach etwa einer Windung entsteht ca. in Windungsmitte eine Kante. Der Bereich zwischen Kante und apikaler Naht liegt anfangs horizontal und ist später zunehmend abgeschrägt. Der Schalenteil abapikal von der Kante steht senkrecht. Auf der letzten Windung verschwindet die Kante und der Umriss wird gleichmäßig konvex.

Zwischen apikaler Naht und Kante werden erst eine (direkt unter der Naht), dann durch Einschaltungen bis zu vier Spiralrippen angelegt. Auch abapikal von der Kante wächst die Zahl der Spiralrippen von anfangs einer auf vier. Die Axialrippen sind auf den ersten Windungen weitständig und relativ kräftig mit großen Höckern auf der Kante. Bei etwa gleichen Abständen werden sie später schwächer und die Höcker kleiner. Die mäßig konvexe Basis geht im Alter gerundet in die Windungsflanken über. Sie ist mit mehreren weiteren Spiralrippen bedeckt, die nahe der Basismitte undeutlich werden. Axialrippen höckern die Spiralrippen. Die Zahl der Axialrippen wird abapikal von der (kaum noch kenntlichen) Kante durch Einschaltungen verdoppelt. Einige Rippen werden nahe des Nabels wulstig verstärkt. Der Nabel ist eng, aber deutlich. Die stets beschädigte Mündung ist rundlich. Die columellare Innenlippe und deren Übergang in den basalen Mündungsrand sind halbmondförmig verbreitert.

Bemerkungen. – TATE (1870) beschrieb *Turbo admirandus* aus der Jamesoni-Zone (tiefes unteres Pliensbachium), also aus etwas jüngeren Schichten. Aus dem Natural History Museum London liegen dem Verfasser mehrere Exemplare einer so bestimmten Art aus dem „Lower Lias“ vor, teilweise präziser als aus der „Valdani Zone“ (mittleres unteres Pliensbachium) stammend etikettiert. Sie lassen keine Unterschiede zur Art aus der Betakalkbank Süddeutschlands erkennen. Demnach hatte die Art eine relativ lange Lebensdauer.

Beziehungen. – Möglicherweise identisch mit der von TATE beschriebenen sowie der vorliegenden Art ist *Turbo bifurcatus* MOORE, 1867 aus dem „Middle Lias“ Englands (MOORE 1867: 209). Beschrieben wird eine Verdoppelung der Zahl der Axialrippen, wie sie auch bei *C. admirandus* zu beobachten ist. *T. bifurcatus* hätte die Priorität vor *C. admirandus*. *Turbo theodorii* v. MÜNSTER, 1844 hat ein breiteres und niedrigeres Gehäuse und es fehlt die Verdoppelung der Axialrippen abapikal von der Windungskante.

Unterklasse Caenogastropoda COX, 1959
Ordnung Ptenoglossa GRAY, 1853
Überfamilie Zygopleuroidea WENZ, 1938
Familie Zygopleuridae WENZ, 1938
Unterfamilie Zygopleurinae WENZ, 1938

Gattung *Levipleura* GRÜNDEL & NÜTZEL, 1998

Typusart: *Melania blainvillei* v. MÜNSTER, 1844; Pliensbachium; Süddeutschland.

Levipleura sp. 1
Taf. 4, Fig. 4–6

Material: 19 Gehäuse, Juvenile und Bruchstücke (SMNS 66787–66789 sowie Sammlung JÄGER).

Beschreibung. – Das auf Taf. 4, Fig. 6 abgebildete Exemplar ist mit ca. 10,5 Windungen (einschließlich dem Protoconch) 8,2 mm hoch. Die Art wurde noch etwas größer. Das Gehäuse ist vielwindig und schlank. Der hoch konische, glatte Protoconch besteht aus reichlich 4 Windungen und ist 0,8 mm hoch. Die Teleoconchwindungen sind schwach konvex, die Nähte wenig eingetieft. Die Skulptur besteht aus schwach opisthoclinen, mehr oder weniger stark opisthocyrten Axialrippen. Diese sind schmal, die Zwischenräume breit. Auf späteren Windungen sind ca. 25 Axialrippen ausgebildet. Sie sind unter der apikalen Naht schwach verdickt. Im Verlauf der Ontogenese werden sie nicht abgeschwächt. Auf der konvexen Basis klingen sie rasch aus. Dicht oberhalb der abapikalen Naht ist eine nicht immer erkennbare schwache Spiralfurche ausgebildet. Die langovale Mündung ist stets beschädigt.

Beziehungen. – *Turritella impressa* Terquem & Piette, 1868 (Angulata-Zone) hat bei großer Ähnlichkeit ein schlankeres Gehäuse. *Procerithium henrici* Martin sensu Dareste de la Chavanne (1912) (Infralias) hat stärker konvexe Flanken und tiefere Nähte, pro Windung sind 14 Axialrippen ausgebildet. Ähnliche Unterschiede bestehen zu *Zygopleura capricornu* McDonald & Trueman, 1921 (Capricornu-Zone). *Levipleura blainvillei* (v. Münster, 1844) (oberes Pliensbachium) hat stärker konvexe Windungen mit tieferen Nähten, weniger Axialrippen pro Windung, und die Skulptur wird spätontogenetisch abgebaut (siehe Gründel & Nützel 1998).

Levipleura sp. 2

Taf. 4, Fig. 3

Material: Ein unvollständiges Gehäuse (SMNS 66786).

Beschreibung. – Das aus 7,5 Windungen bestehende Bruchstück (die Spitze des Gehäuses fehlt) ist 10,5 mm hoch. Im Unterschied zur *Levipleura* sp. 1 sind nur ca. 16 Axialrippen pro Windung ausgebildet, und diese sind wulstiger und breiter (etwa ebenso breit oder breiter wie ihre Zwischenräume), und es fehlt die apikale Verdickung. Sie sind nicht oder nur sehr schwach opisthocyrt. Die Basis ist kaum konvex und durch eine gerundete Kante winklig abgesetzt.

Beziehungen. – *Chemnitzia transversa* Blake, 1872 in der Darstellung von Tate & Blake 1876 (Angulata-Zone) hat nur 10 und stärker wulstige Axialrippen pro Windung, die Basis ist nicht winklig abgesetzt. *Chemnitzia poleymiaca* Dumortier, 1864 (Infralias) hat ein breiteres Gehäuse und etwas weniger Axialrippen pro Windung (12–14).

Gattung *Katosira* Koken, 1892

Typusart: *Chemnitzia periniana* d'Orbigny, 1851; Pliensbachium; Frankreich.

Katosira basistriata n. sp.

Taf. 4, Fig. 7

Holotypus: Das auf Taf. 4, Fig. 7 abgebildete Exemplar (SMNS 66790).

Paratypen: 11 Gehäuse und Bruchstücke (Sammlung Jäger).

Locus typicus: Mittelstreifen der B 27 in einer Senke zwischen Bisingen und Hechingen (Baden-Württemberg).

Stratum typicum: Betakalkbank, obere Obtusum-Zone, oberes Sinemurium.

Derivatio nominis: Nach den auf die Basis beschränkten Spiralrippen.

Diagnose. – Axialrippen unter der apikalen Naht schwach verdickt, auf der letzten Windung parasigmoidal; späte Windungen mit 25–30 Axialrippen; Basis stark konvex, mit 4–5 breiten Spiralrippen.

Diagnosis. – Axial ribs weakly thickened on their adapical end, on the last whorl parasigmoidal; late whorls with 25–30 axial ribs; base strongly convex, covered with 4–5 broad spiral ribs.

Beschreibung. – Der Holotypus ist mit ca. 10 Windungen (einschließlich dem Protoconch) 8,3 mm hoch. Das schlanke Gehäuse hat schwach konvexe Windungen mit eingetieften Nähten. Der glatte Protoconch besteht aus ca. 4 Windungen und ist 0,7 mm hoch. Die Skulptur des Teleoconchs besteht aus anfangs geraden, später opisthocyrten Axialrippen. Auf späten Windungen sind 25–30 Axialrippen ausgebildet. Sie sind etwas schmaler als ihre Zwischenräume. Deutliche Spiralrippen fehlen auf den Windungsflanken. Nur dicht unter der apikalen Naht sind die Axialrippen etwas verdickt und werden durch eine schwache Spiralrippe verbunden. Die konvexe Basis ist nicht abgesetzt und trägt 4–5 breite Spiralrippen. Die Axialrippen schwächen auf ihr rasch zu etwas betonten, prosocyrten Anwachslinien ab. Die Mündung ist langoval und läuft abapikal in einen Kanal aus.

Beziehungen. – Der in Gestalt und Axialskulptur ähnlichen *Cerithium henrici* Martin, 1862 („Infra-Lias“ = Hettangium) fehlen Spiralrippen, die Axialrippen sind weniger zahlreich. *Zygopleura* cf. *taeniata* (Deslongchamps, 1842) sensu McDonald & Trueman 1921 (Carixium) hat zahlreichere und nicht so deutlich parasigmoidale Axialrippen. *Cerithium planicostatum* Moore, 1867 (Lias) hat keine apikal verdickten Axialrippen, Flanken und Basis sind weniger stark konvex, die Basis ist mit „faint striae“ (Moore 1867: 542) bedeckt.

Familie Protorculidae Bandel, 1991

Gattung *Protorcula* Kittl, 1894

Typusart: *Turritella subpunctata* v. Münster, 1841; obere Trias; Alpen.

Protorcula? *quadricostata* n. sp.

Taf. 4, Fig. 8–9; Taf. 5, Fig. 1

Holotypus: Das auf Taf. 5, Fig. 1 abgebildete Exemplar (SMNS 66793).

Paratypen: 22 Bruchstücke (SMNS 66791, 66792 sowie Sammlung Jäger).

Locus typicus: Mittelstreifen der B 27 in einer Senke zwischen Bisingen und Hechingen (Baden-Württemberg).

Stratum typicum: Betakalkbank, obere Obtusum-Zone, oberes Sinemurium.

Derivatio nominis: Benannt nach den vier kräftigen Spiralrippen auf jeder Windung.

Diagnose. – Windungen mit zwei den Nähten benachbarten Spiralwülsten; jede Wulst mit zwei kräftigen Spiralrippen und kurzen Axialrippen; die Axialrippen der apikalen Wulst sind orthoclin und zahlreicher als die opisthoclinen Axialrippen der abapikalen Wulst.

Diagnosis. – Teleoconch whorls with two strong spiral ledges near to the sutures; each ledge with two strong spiral ribs and short axial ribs; on the adapical ledge the axial ribs are orthocline and more numerous than the opisthocline axial ribs on the abapical ledge.

Beschreibung. – Der Holotypus (Taf. 5, Fig. 1) ist 7,5 mm hoch. Das Gehäuse ist sehr schlank und vielwindig. Die Windungsflanken sind schwach konkav, die Nähte kaum eingesenkt. Der Protoconch ist nicht erhalten. Beide Nähte werden von einer deutlichen Wulst begleitet. Auf jeder Wulst verlaufen 2 Spiralrippen. Beide

Wülste werden von kurzen Axialrippen gehöckert, die in der Windungsmitte nicht miteinander verbunden sind. Die Axialrippen der apikalen Wulst sind gerade, orthoclin und zahlreich (21 auf der letzten Windung des Holotypus). Die Axialrippen der abapikalen Wulst sind opisthoclin, weitständiger und weniger zahlreich (13 am Holotypus). Im konkaven Bereich zwischen beiden Wülsten sind 2 Spiralrippen ausgebildet. Die Anwachslinien verlaufen parasigmoidal mit vorgezogenem abapikalen Teil. Die flache Basis ist an der Grenzspiralrippe (die etwas oberhalb der Naht sichtbar wird) winklig abgesetzt. Es folgen eine weitere kräftige und eine schwache Spiralrippe. Die stets beschädigte Mündung ist breit oval mit deutlichem abapikalen Kanal.

Bemerkungen. – Vollständige Gehäuse liegen nicht vor. Die Bruchstücke haben typisch protorculiden Habitus. Ungewöhnlich für *Protorcula* sind die beiden Spiralrippen auf jeder der beiden Wülste und die unterschiedliche Ausbildung der Axialrippen auf diesen. Durch diese Merkmalskombination wird die Art unverwechselbar. Da der Protoconch unbekannt ist, erfolgt die Zuweisung zu *Protorcula* mit Vorbehalt.

Beziehungen. – Bei *Cerithiella*(?) *terebellopsis* COSSMANN, 1913 (Pliensbachium) ist nur die apikale Wulst zweigeteilt und zudem kräftiger als die abapikale, die Windungen sind niedriger und auf der Basis sind 3–4 Spiralrippen ausgebildet.

Überfamilie Pseudomelanoidea HOERNES, 1884
Familie Pseudomelaniidae HOERNES, 1884

Gattung *Pseudomelania* PICTET & CAMPICHE, 1862

Typusart: *Pseudomelania gresslyi* PICTET & CAMPICHE, 1862; Neocom; Schweiz.

Pseudomelania sp.
Taf. 4, Fig. 2

Material: Ein Exemplar (SMNS 66785).

Beschreibung. – Das aus 8 Windungen bestehende Exemplar (die Gehäusespitze fehlt) ist 7,5 mm hoch. Die Windungen sind niedrig und breit sowie schwach konvex. Die Nähte sind eingetieft (angedeutete Rampe). Eine Skulptur fehlt. Die konvexe Basis ist nicht abgesetzt. Die Anwachslinien verlaufen auf den Windungsflanken opisthocyrt, auf der Basis prosocyrt. Die Mündung ist breitoval und apikal wohl etwas zugespitzt. Ein abapikaler Kanal ist vorhanden.

Beziehungen. – Der Holotypus der ähnlichen *Pseudomelania phidias* (D'ORBIGNY, 1851) ist ein Steinkern (FISCHER & WEBER 1997: 13) und stammt aus dem oberen Hettangium oder tiefen Sinemurium. Die Art wird größer, die Windungen sind höher im Verhältnis zur Breite und stärker konvex, es fehlt die Andeutung einer Rampe.

Caenogastropode unsicherer taxonomischer Stellung
Taf. 5, Fig. 5

Material: Ein Bruchstück (SMNS 66797).

Beschreibung. – Das Bruchstück ist 7,3 mm hoch und schlecht erhalten. Die Windungen sind stark konvex mit eingetieften Nähten. Die Gehäusespitze fehlt. Das Bruchstück beginnt mit einer glatten(?) halben Windung. Dann setzen mindestens 4 Spiralrippen ein, später sind es 5. Die 3 abapikalen Spiralrippen sind etwas kräftiger als die beiden apikalen. Eine deutliche Axialskulptur fehlt. Die Anwachslinien verlaufen prosoclin und schwach prosocyrt. Sie sind etwas verstärkt. Auch auf der konvexen Basis sind Spiralrippen ausgebildet. Weitere Details sind nicht erhalten.

Bemerkungen. – In Gestalt und Skulptur bestehen Ähnlichkeiten zur Gattung *Turritelloidea* WALTHER, 1951 (Heterobranchia, Gordenellidae). Es fehlt das frühontogenetische mathildide Skulpturstadium. Auch die Anwachslinien verlaufen anders (nicht opisthocyrt, wie für die Mathildoidea charakteristisch).

Unterklasse Heterobranchia GRAY, 1840
Ordnung Allogastropoda HASZPRUNAR, 1985
Überfamilie Mathildoidea DALL, 1889
Familie Mathildidae DALL, 1889

Gattung *Tricarilda* GRÜNDEL, 1973

Typusart: *Mathilda (Tricarilda) plana* GRÜNDEL, 1973; Callovium; nordwestliches Polen.

Tricarilda sp.
Taf. 5, Fig. 7–8

Material: 3 Bruchstücke (SMNS 66799, 66800 sowie Sammlung JÄGER).

Beschreibung. – Das größte Bruchstück ist mit 7,5 Windungen 6 mm hoch. Der Protoconch ist nicht erhalten. Das Gehäuse ist schlank mit wenig betonten Nähten. Die frühesten Windungen zeigen eine schwache apikale Spiralrippe sowie zwei kräftigere etwa in Windungsmitte und oberhalb der abapikalen Naht. Die letzteren bleiben auch später am kräftigsten und werden abapikalwärts verlagert. Der Bereich zwischen apikaler und mittlerer primärer Spiralrippe verbreitert sich und wird konkav. Beidseitig von der apikalen Spiralrippe wird je eine sekundäre Spiralrippe gebildet. Ein Bruchstück von einem späteren ontogenetischen Stadium zeigt, dass während der Ontogenese noch weitere Spiralrippen gebildet werden. Zahlreiche eng stehende verstärkte Anwachslinien queren die Spiralrippen ohne Höckerbildung. Sie sind deutlich opisthocyrt. Ihr hinterster Punkt liegt im Bereich der mittleren primären Spiralrippe. Die flache Basis ist an einer kräftigen Grenzspiralrippe winklig abgesetzt. Auf sie folgen mindesten 6 schwächer werdende Spiralrippen. Die verstärkten Anwachslinien verlaufen auf der Basis prosocyrt. Die Mündung ist breitoval.

Beziehungen. – Die unvollständige Erhaltung macht einen sicheren Vergleich mit beschriebenen Arten unmöglich. *Turritella dunkeri* TERQUEM, 1855 sensu TATE & BLAKE 1876 (oberes Hettangium bis unteres Sinemurium) ist schlanker, hat konvexe Windungen mit eingetieften Nähten, es fehlt die Konkavität des Seitenumrisses zwischen apikaler und mittlerer primärer Spiralrippe, die mittlere Primärspiralrippe kantet den Seitenumriss etwas. Ähnliche Unterschiede bestehen zu *Promathildia (Clathrobaculus) sinemuriensis* (MARTIN, 1862) sensu COSSMANN (1913), die Basis soll zudem skulpturlos sein. *Tricarilda*? sp. sensu GRÜNDEL (1999) (oberstes Pliensbachium) fehlt die Konkavität zwischen apikaler und mittlerer Primärspiralrippe, die Basis hat weniger und kräftigere Spiralrippen.

Mathildidae sp.

Taf. 5, Fig. 6

Material: Ein Bruchstück (SMNS 66798).

Beschreibung. – Das aus 4 Windungen bestehende, nur mäßig erhaltene Bruchstück ist 3,8 mm hoch. Die Gehäusespitze fehlt. Das schlanke Gehäuse hat konvexe Windungen mit eingetieften Nähten. Auf den Flanken sind anfangs 3, später 7 Spiralrippen ausgebildet. Eine etwa in Windungsmitte und eine oberhalb der abapikalen Naht gelegene Spiralrippe sind anfangs kräftiger und kanten den Umriss etwas. Später sind sie kaum mehr betont. Sehr zahlreiche eng stehende Axialrippen sind schwach opisthocyrt und höckern die Spiralrippen. Sie sind nur wenig schwächer als diese. Die mäßig konvexe Basis ist an der Grenzspiralrippe etwas abgesetzt. Weitere Details sind nicht erkennbar.

Beziehungen. – Für detaillierte Vergleiche ist die Art zu unvollständig erhalten. *Promathildia turritella* (DUNKER, 1846) sensu MEIER & MEIERS (1988) (unteres Hettangium) hat 5 Spiralrippen und die Axialrippen sind schwächer. Auch die von BRÖSAMLEN (1909) beschriebene gleichnamige Art hat viel schwächere Axialrippen sowie zwei bis drei betonte Spiralrippen.

3. Schlussbemerkungen

BRÖSAMLEN (1909) führte aus der Betakalkbank nur 3 Arten an. Seine *Trochus percarinatus* n. sp. wird unter „Bemerkungen“ bei der Art *Trypanotrochus*? *broesamleni* n. sp. diskutiert und als nomen dubium gewertet. Das Original der *Trochus betacalcis* QUENSTEDT, 1856 zu QUENSTEDT 1884 (Taf. 201, Fig. 89) (und wahrscheinlich auch zu QUENSTEDT 1856 und BRÖSAMLEN 1909, Taf. 17, Fig. 14) konnte in Tübingen gesehen werden. Es liegt zur Hälfte im umgebenden Gestein. Die freiliegende Hälfte ist teils als Steinkern, teils mit Schale erhalten. Die Schalenerhaltung ist schlecht, Details der Skulptur sind vielfach nicht erkennbar. Die Mündung ist gleichfalls nicht erhalten. Das Original lässt wichtige Merkmale für eine artliche Bestimmung nicht erkennen. Auch diese Art ist als nomen dubium zu werten. *Turbo euomphalus* QUENSTEDT, 1856 ist mit keiner der im vorliegenden Material auftretenden Arten gleichzusetzen (siehe „Bemerkungen“ bei *Ataphrus naricopsiformis* n. sp.).

In den vergangenen fast 100 Jahren sind weitere Funde aus der Betakalkbank nicht bekannt geworden. Dies unterstreicht die Bedeutung der neu entdeckten Fauna. Sie schließt eine Lücke zwischen der reichhaltigeren Fauna des Lias α (oberes Hettangium bis unteres Sinemurium; vgl. Gründel 2003) und der ebenfalls deutlich artenreicheren, weit verbreiteten Fauna des Pliensbachiums. Über Fundumstände, Erhaltung und Gewinnung der Gastropoden ist in der Einleitung das Erforderliche gesagt worden.

Zur Auswertung lagen 156 Exemplare vor, die sich auf 17 Arten verteilen. Mit 10 Arten und 95 Exemplaren sind die Archaeogastropoda am stärksten vertreten. Sie stellen mit *Ataphrus euomphalus* auch die häufigste Art (42 Exemplare). Es folgen mit 6 Arten und 57 Exemplaren die Caenogastropoda. Die Heterobranchia schließlich sind nur mit 2 Arten und 4 Exemplaren vertreten.

Die Zusammensetzung der Fauna weicht deutlich von der der älteren und jüngeren Faunen ab. Das hat wohl fazielle Gründe. So stammen die Faunen des Pliensbachiums Frankens weitgehend aus tonig-siltigen Sedimenten des offshore-Bereiches. Die Bildung der Betakalkbank erfolgte dagegen in geringer Wassertiefe, und statt der Tone wurde Kalkschlamm sedimentiert (Brandt 1985). Vertreter der Gattungen *Anticonulus*, *Trypanotrochus*, *Costataphrus* und *Protorcula* sind dem Verfasser aus dem unteren Jura Deutschlands bisher nicht bekannt geworden. Auffallend ist auch das starke Zurücktreten der Heterobranchia. Die im Pliensbachium so arten- und individuenreichen Opisthobranchia fehlen ganz.

4. Literatur

Brandt, K. (1985): Sea-level changes in the Upper Sinemurian and Pliensbachian of Southern Germany. – In: Bayer, U. & Seilacher, A. (Hrsg.): Sedimentary and evolutionary cycles: 113–126; Berlin, Heidelberg, New York, Tokyo (Springer-Verlag).

Brösamlen, R. (1909): Beitrag zur Kenntnis der Gastropoden des schwäbischen Jura. – Palaeontographica, **56**: 177–321.

Chartron, C. & Cossmann, M. (1902): Note sur l'Infralias de la Vendée et specialement sur un gisement situé dans la commune du Simon-la-Vineuse. – Bulletin de la Société géologique de France, (4) **2**: 163–203.

Cossmann, M. (1913): Contributions à la paléontologie française des terrains jurassiques. III. Cerithiacea et Loxonematacea. – Mémoires de la Société géologique de France, Paléontologie, **46**: 1–263.

Dareste de la Chavanne, J. (1912): Monographie paléontologique d'une faune de l'Infralias du Nivernais méridional. – Bulletin de la Société géologique de France, (4) **12**: 550–604.

Fischer, J.-C. & Weber, Ch. (1997): Révision critique de la paléontologie Française d'Alcide d'Orbigny. Vol. II: Gastropodes jurassiques. – 300 S.; Paris (Masson).

Goldfuss, A. (1826–1844): Petrefacta Germaniae. – 1. Teil (1826–1833): 252 S.; 2. Teil (1834–1840): 312 S.; 3. Teil (1841–1844): 128 S.; Düsseldorf (Arnz & Comp.).

Gründel, J. (1999): Gastropoden aus dem höheren Lias von Grimmen, Vorpommern (Deutschland). – Archiv für Geschiebekunde, **2** (9): 629–672.

Gründel, J. (2000): Archaeogastropoda aus dem Dogger Norddeutschlands und des nordwestlichen Polens. – Berliner geowissenschaftliche Abhandlungen, Reihe E, **34**: 205–253.

Gründel, J. (2003): Gastropoden aus dem unteren Lias (Ober-Hettangium bis Unter-Sinemurium) Südwestdeutschlands. – Stuttgarter Beiträge zur Naturkunde, Serie B, **340**: 55 S.

Gründel, J. & Nützel, A. (1998): Gastropoden aus dem oberen Pliensbachium (Lias δ_2, Zone des *Pleuroceras spinatum*) von Kalchreuth östlich Erlangen (Mittelfranken). – Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie, **38**: 63–96.

Hägele, G. (1997): Juraschnecken. – Fossilien, Sonderband, **11**: 144 S.

Hoffmann, K. (1964): Die Stufe des Lotharingien (Lotharingium) im Unterlias Deutschlands und allgemeine Betrachtungen über das „Lotharingien". – Colloque Jurassique in Luxembourg 1962: 135–160.

Knight, J. B., Cox, L. R., Keen, A. M., Batten, R. L., Yochelson, E. L. & Robertson, R. (1960): Gastropoda – Systematic descriptions. – In: Moore, R. C. & Pitrat, C. W. (Hrsg.): Treatise on Invertebrate Paleontology, Part I, Mollusca 1, S. I169–I310; Lawrence (Geological Society of America, University of Kansas Press).

Kuhn, O. (1936): Die Fauna des Amaltheentons (Lias δ) in Franken. – Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B, Beilagen-Band **75**: 231–311.

McDonald, A. J. & Trueman, A. E. (1921): The evolution of certain Liassic gastropods, with special reference to their use in stratigraphy. – Quarterly Journal of the Geological Society London, **77**: 297–344.

Meier, H. & Meiers, K. (1988): Die Gastropodenfauna der „Angulata-Zone" des Steinbruchs „Reckingerwald" bei Brouch. – Travaux scientifiques du Musée National d'Histoire Naturelle de Luxembourg, **13**: 1–88.

Moore, C. (1867): On the Middle and Upper Lias of the South West of England. – Proceedings Somersetshire Archaeological and Natural History Society, **13**: 119–244.

Quenstedt, F. A. (1856–1857): Der Jura. 1. Lfg. (1856): 1–208, Taf. 1–24; 2. Lfg. (1856): 209–368, Taf. 24–48, 1 Profiltafel (Lias); 3. Lfg. (1857): 369–576, Taf. 49–72, 1 Profiltafel (Brauner Jura); 4. Lfg. (1857): I–IV + 577–842, Taf. 73–100, 1 Profiltafel (Weißer Jura); Tübingen (Laupp & Siebeck).

Quenstedt, F. A. (1881–1884): Petrefaktenkunde Deutschlands. Erste Abteilung, Band 7: Gasteropoden. 867 S.; Leipzig (Fues's).

Schnittmann, F. X. (1966): Verzeichnis der im Lias und untersten Dogger bei Ehenfeld gefundenen Versteinerungen, sowie Beschreibung und Abbildung der neuen Arten und Varietäten. – Acta Albertina Ratisbonensia, **26**: 71–88.

Söll, H. (1956): Stratigraphie und Ammonitenfauna des mittleren und oberen Lias-β (Lotharingien) in Mittel-Württemberg. – Geologisches Jahrbuch, **72**: 367–434.

Stoliczka, F. (1861): Über die Gastropoden und Acephalen der Hierlatz-Schichten. – Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der k. Akademie der Wissenschaften Wien, **43**, I. Abtheilung: 157–204.

Tate, R. (1870): On the palaeontology of the Junction beds of the Lower and Middle Lias in Gloucestershire. – The Quarterly Journal of the Geological Society of London, **26**: 394–408.

Tate, R. & Blake, J. F. (1876): The Yorkshire Lias. 475 S.; London (John von Vorst).

Urlichs, M. (1977): The Lower Jurassic in Southwestern Germany. – Stuttgarter Beiträge zur Naturkunde, Serie B, **24**: 41 S.

Wilson, E. (1887): British Liassic Gasteropoda. – Geological Magazin, (3) **4**: 194–202.

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Tafel 1

Fig. 1. *Ptychomphalus* sp. (SMNS 66774); **a**: Dorsalansicht; **b**: Seitenansicht; **c**: Ventralansicht (Breite des Gehäuses 10,2 mm).

Fig. 2. *Ptychomphalus* sp. (SMNS 66775); **a**: Dorsalansicht (Breite des Gehäuses 15 mm); **b**: Detail von Fig. 2a (Breite der Windung 5,2 mm).

Fig. 3. *Metriomphalus*? sp., cf. *thetis* (v. MÜNSTER, 1844) (SMNS 66776); **a**: oberer Teil des Gehäuses in Seitenansicht (Höhe 4,3 mm); **b**: Detail der Fig. 3a (Höhe der Windung 1,6 mm).

Fig. 4. *Metriomphalus*? sp., cf. *thetis* (v. MÜNSTER, 1844) (SMNS 66777); **a**: Seitenansicht; **b**: Ventralansicht (Höhe 9,5 mm, Breite 9 mm); **c**: Detail von Fig. 4a (Höhe der Windung 4 mm).

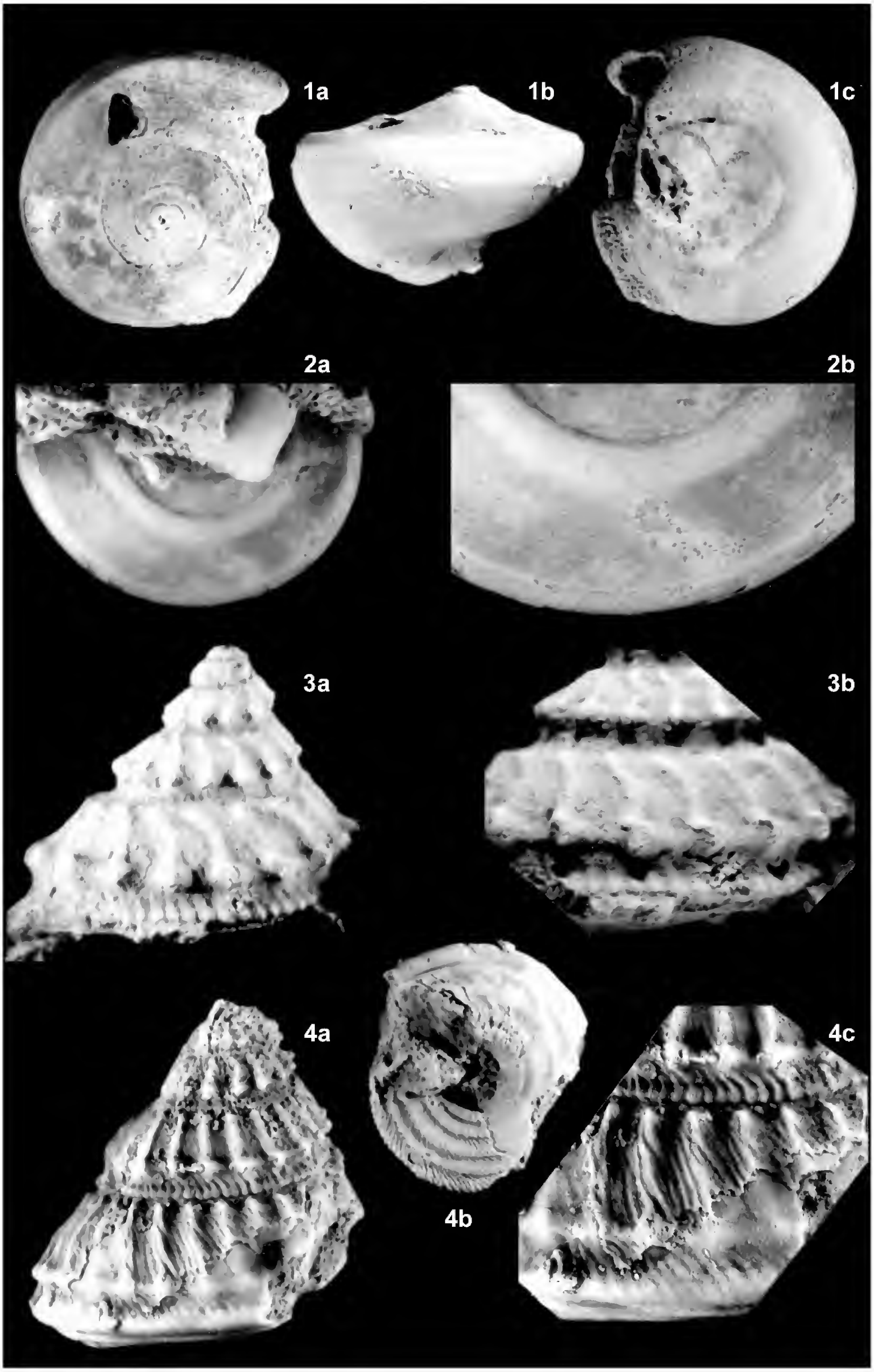
Plate 1

Fig. 1. *Ptychomphalus* sp. (SMNS 66774); **a**: dorsal view; **b**: side view; **c**: ventral view (width of the shell 10.2 mm).

Fig. 2. *Ptychomphalus* sp. (SMNS 66775); **a**: dorsal view (width of the shell 15 mm); **b**: detail of Fig. 2a (width of the whorl 5.2 mm).

Fig. 3. *Metriomphalus*? sp., cf. *thetis* (v. MÜNSTER, 1844) (SMNS 66776); **a**: upper part of the shell in side view (height 4.3 mm); **b**: detail of Fig. 3a (height of the whorl 1.6 mm).

Fig. 4. *Metriomphalus*? sp., cf. *thetis* (v. MÜNSTER, 1844) (SMNS 66777); **a**: side view; **b**: ventral view (height 9.5 mm, width 9 mm); **c**: detail of Fig. 4a (height of the whorl 4 mm).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Tafel 2

Fig. 1. *Anticonulus jaegeri* n. sp., Holotypus (SMNS 66778); **a**: Seitenansicht mit Mündung; **b**: Ventralansicht; **c**: Seitenansicht ohne Mündung (Höhe 6,3 mm, Breite 5 mm); **d**: Gehäusespitze in Seitenansicht (Höhe 1,1 mm).

Fig. 2. *Trypanotrochus*? *broesamleni* n. sp., Holotypus (SMNS 66779); **a**: Seitenansicht mit Mündung; **b**: Seitenansicht ohne Mündung (Höhe 7,8 mm, Breite 6,2 mm); **c**: Ventralansicht.

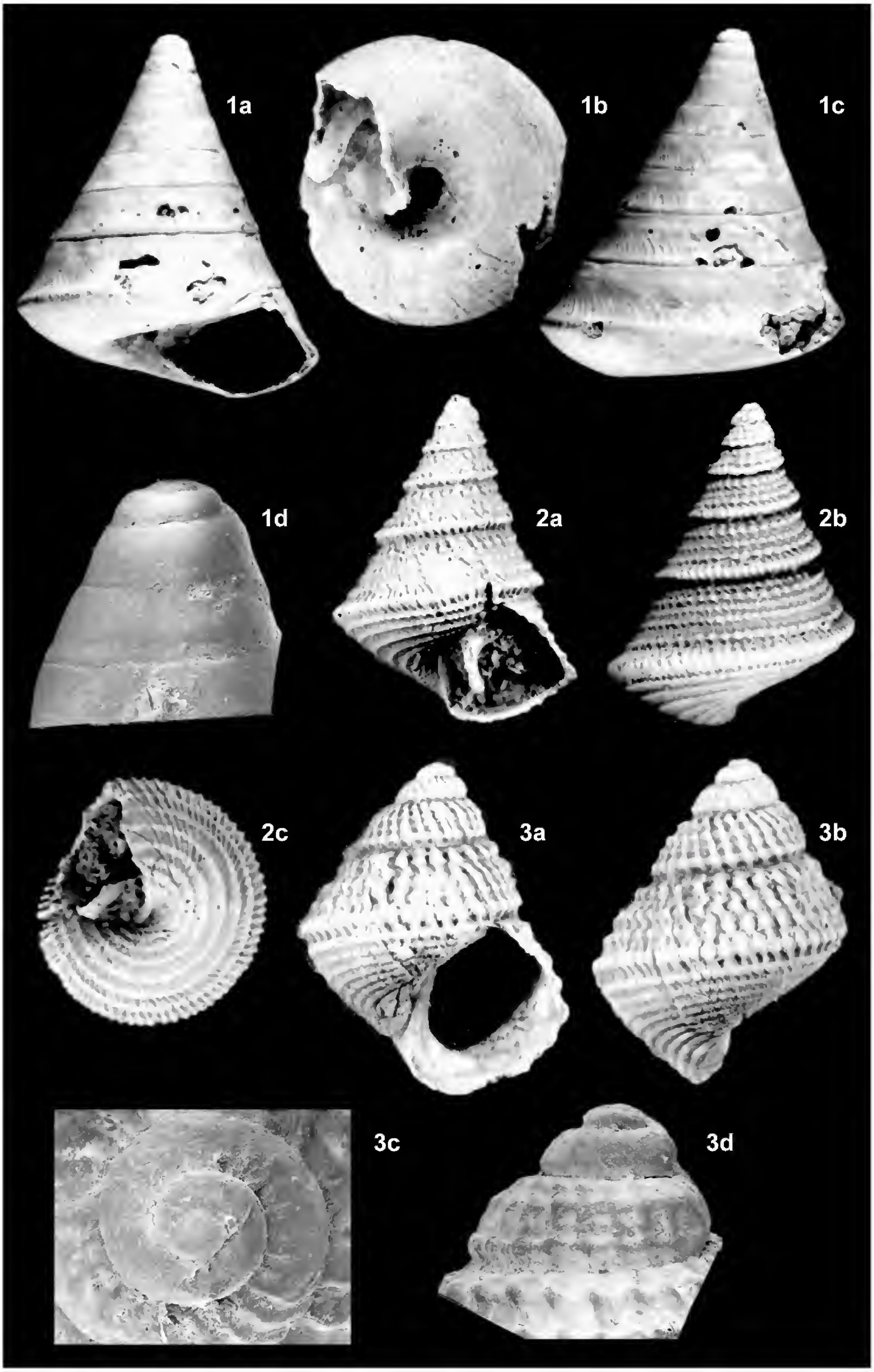
Fig. 3. *Eucycloscala* sp., cf. *brunhuberi* (SCHNITTMANN, 1966) (SMNS 66780); **a**: Seitenansicht mit Mündung; **b**: Seitenansicht ohne Mündung (Höhe 5,2 mm); **c**: Gehäusespitze in Dorsalansicht (Breite 1 mm); **d**: Gehäusespitze in Seitenansicht (Höhe 1,4 mm).

Plate 2

Fig. 1. *Anticonulus jaegeri* n. sp., holotype (SMNS 66778); **a**: side view with aperture; **b**: ventral view; **c**: side view without aperture (height 6.3 mm, width 5 mm); **d**: top of the shell in side view (height 1.1 mm).

Fig. 2. *Trypanotrochus*? *broesamleni* n. sp., holotype (SMNS 66779); **a**: side view with aperture; **b**: side view without aperture (height 7.8 mm, width 6.2 mm); **c**: ventral view.

Fig. 3. *Eucycloscala* sp., cf. *brunhuberi* (SCHNITTMANN, 1966) (SMNS 66780); **a**: side view with aperture; **b**: side view without aperture (height 5.2 mm); **c**: top of the shell in dorsal view (width 1 mm); **d**: top of the shell in side view (height 1.4 mm).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Tafel 3

Fig. 1. *Gerasimovcyclus triplicatus* (Martin, 1862)? (SMNS 66781); **a**: Seitenansicht mit Mündung; **b**: Seitenansicht ohne Mündung (Höhe 8 mm).

Fig. 2. *Lewisiella ventrocostata* n. sp., Paratypus (SMNS 66782); **a**: Ventralansicht (Breite 4,8 mm); **b**: Gehäusespitze in Dorsalansicht (Höhe 1 mm).

Fig. 3. *Lewisiella ventrocostata* n. sp., Holotypus (SMNS 66783); **a**: Seitenansicht mit Mündung; **b**: Seitenansicht ohne Mündung (Höhe 5,7 mm).

Fig. 4. *Costataphrus admirandus* (Tate, 1870) (SMNS 66784); **a**: Seitenansicht (Breite 3,9 mm); **b**: Gehäusespitze in Dorsalansicht (Breite 2,1 mm); **c**: Gehäusespitze in Seitenansicht (Höhe 1,7mm); **d**: Ventralansicht (Breite 3,9 mm).

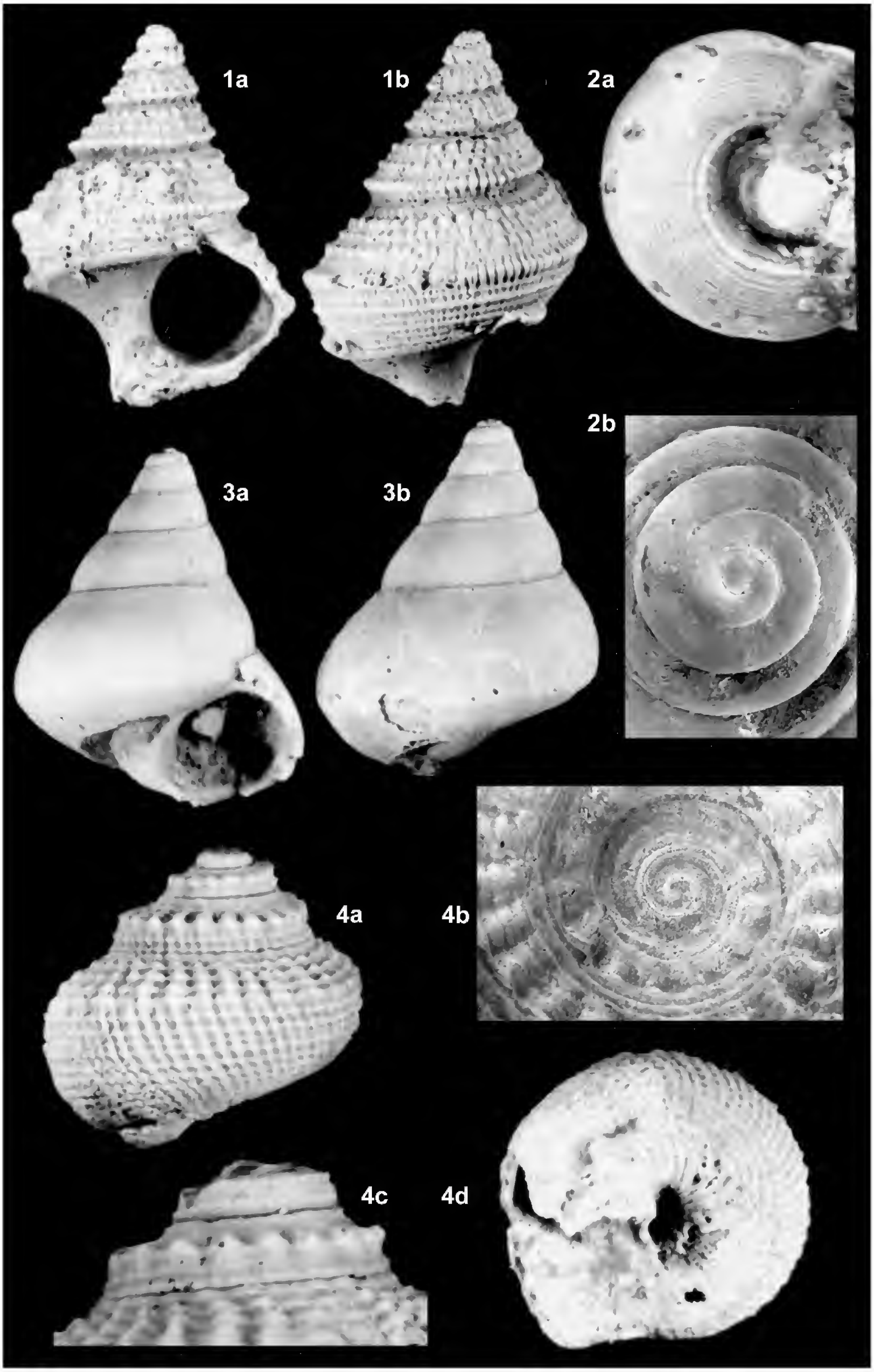
Plate 3

Fig. 1. *Gerasimovcyclus triplicatus* (Martin, 1862)? (SMNS 66781); **a**: side view with aperture; **b**: side view without aperture (height 8 mm).

Fig. 2. *Lewisiella ventrocostata* n. sp., paratype (SMNS 66782); **a**: ventral view (width 4.8 mm); **b**: top of the shell in dorsal view (height 1 mm).

Fig. 3. *Lewisiella ventrocostata* n. sp., holotype (SMNS 66783); **a**: side view with aperture; **b**: side view without aperture (height 5.7 mm).

Fig. 4. *Costataphrus admirandus* (Tate, 1870) (SMNS 66784); **a**: side view (width 3.9 mm); **b**: top of the shell in dorsal view (width 2.1 mm); **c**: top of the shell in side view (height 1.7 mm); **d**: ventral view (width 3.9 mm).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Tafel 4

Fig. 1. *Costataphrus admirandus* (Tate, 1870) (SMNS 66784); Seitenansicht (Breite 3,9 mm).

Fig. 2. *Pseudomelania* sp. (SMNS 66785). **a**: Seitenansicht ohne Mündung; **b**: Seitenansicht mit Mündung (Höhe 7,5 mm).

Fig. 3. *Levipleura* sp. 2 (SMNS 66786); Seitenansicht (Höhe 10,4 mm).

Fig. 4. *Levipleura* sp. 1 (SMNS 66787); Seitenansicht (Höhe 3,1 mm).

Fig. 5. *Levipleura* sp. 1 (SMNS 66788); Seitenansicht (Höhe 4,5 mm).

Fig. 6. *Levipleura* sp. 1 (SMNS 66789); **a**: Gehäusespitze in Seitenansicht (Höhe 0,75 mm); **b**: Seitenansicht mit Mündung; **c**: Seitenansicht ohne Mündung (Höhe 8,2 mm).

Fig. 7. *Katosira basistriata* n. sp., Holotypus (SMNS 66790); **a**: Seitenansicht (Höhe 8,3 mm); **b**: Letzte Windung in Seitenansicht (Höhe 3,5 mm); **c**: Gehäusespitze in Seitenansicht (Höhe 0,9 mm).

Fig. 8. *Protorcula*? *quadricostata* n. sp., Paratypus (SMNS 66791); Ventralansicht (Breite 3,2 mm).

Fig. 9. *Protorcula*? *quadricostata* n. sp., Paratypus (SMNS 66792); Seitenansicht (Höhe 4,8 mm).

Plate 4

Fig. 1. *Costataphrus admirandus* (Tate, 1870) (SMNS 66784); side view (width 3.9 mm).

Fig. 2. *Pseudomelania* sp. (SMNS 66785); **a**: side view without aperture; **b**: side view with aperture (height 7.5 mm).

Fig. 3. *Levipleura* sp. 2 (SMNS 66786); side view (height 10.4 mm).

Fig. 4. *Levipleura* sp. 1 (SMNS 66787); side view (height 3.1 mm).

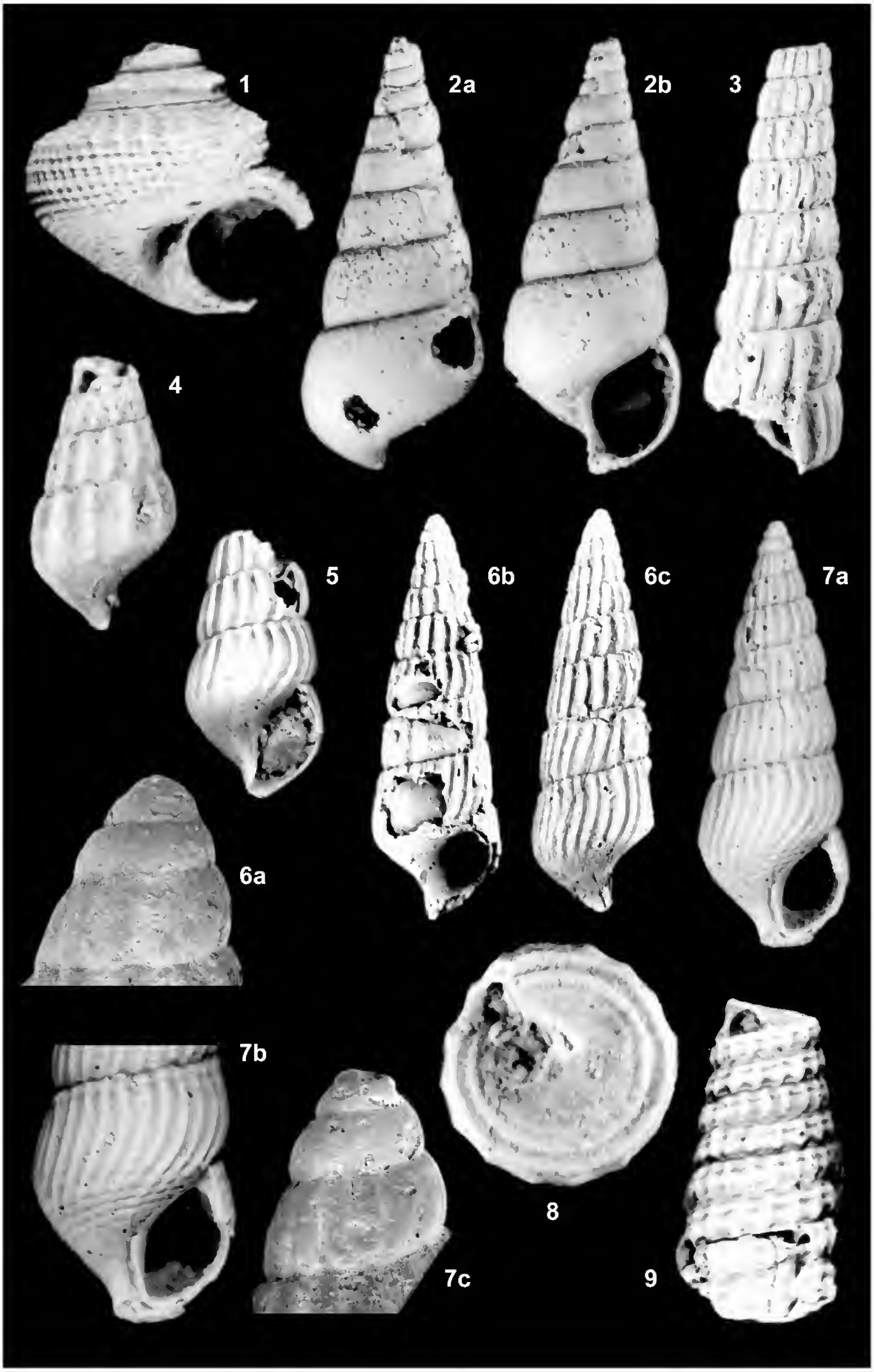
Fig. 5. *Levipleura* sp. 1 (SMNS 66788); side view (height 4.5 mm).

Fig. 6. *Levipleura* sp. 1 (SMNS 66789); **a**: top of the shell in side view (height 0.75 mm); **b**: side view with aperture; **c**: side view without aperture (height 8.2 mm).

Fig. 7. *Katosira basistriata* n. sp., holotype (SMNS 66790); **a**: side view (height 8.3 mm); **b**: last whorl in side view (height 3.5 mm); **c**: top of the shell in side view (height 0.9 mm).

Fig. 8. *Protorcula*? *quadricostata* n. sp., paratype (SMNS 66791); ventral view (width 3.2 mm).

Fig. 9. *Protorcula*? *quadricostata* n. sp., paratype (SMNS 66792); side view (height 4.8 mm).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Tafel 5

Fig. 1. *Protorcula? quadricostata* n. sp., Holotypus (SMNS 66793); **a**: Seitenansicht (Höhe 7,5 mm); **b**: Ausschnitt von Fig. 1a (Höhe 2,6 mm).

Fig. 2. *Ataphrus naricopsiformis* n. sp., Paratypus (SMNS 66794); **a**: Seitenansicht; **b**: Ventralansicht; **c**: Dorsalansicht (Breite 8,2 mm).

Fig. 3. *Ataphrus naricopsiformis* n. sp., Holotypus (SMNS 66795); **a**: Ventralansicht; **b**: Seitenansicht (Breite 3,7 mm).

Fig. 4. *Ataphrus naricopsiformis* n. sp., Paratypus (SMNS 66796); Dorsalansicht (Breite 3,3 mm).

Fig. 5. Caenogastropode unsicherer taxonomischer Stellung (SMNS 66797); Seitenansicht (Höhe 7,3 mm).

Fig. 6. Mathildidae sp. (SMNS 66798); Seitenansicht (Höhe 3,8 mm).

Fig. 7. *Tricarilda* sp. (SMNS 66799); Seitenansicht (Höhe 6 mm).

Fig. 8. *Tricarilda* sp. (SMNS 66800); Ventralansicht (Breite 3,5 mm).

Plate 5

Fig. 1. *Protorcula? quadricostata* n. sp., holotype (SMNS 66793); **a**: side view (height 7.5 mm); **b**: detail of Fig. 1a (height 2.6 mm).

Fig. 2. *Ataphrus naricopsiformis* n. sp., paratype (SMNS 66794); **a**: side view; **b**: ventral view; **c**: dorsal view (width 8.2 mm).

Fig. 3. *Ataphrus naricopsiformis* n. sp., holotype (SMNS 66795); **a**: ventral view; **b**: side view (width 3.7 mm).

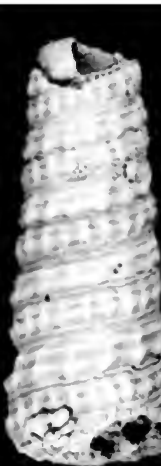
Fig. 4. *Ataphrus naricopsiformis* n. sp., paratype (SMNS 66796); dorsal view (width 3.3 mm).

Fig. 5. Caenogastropod of uncertain taxonomic position (SMNS 66797); side view (height 7.3 mm).

Fig. 6. Mathildidae sp. (SMNS 66798); side view (height 3.8 mm).

Fig. 7. *Tricarilda* sp. (SMNS 66799); side view (height 6 mm).

Fig. 8. *Tricarilda* sp. (SMNS 66800); ventral view (width 3.5 mm).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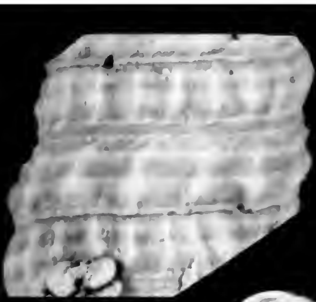
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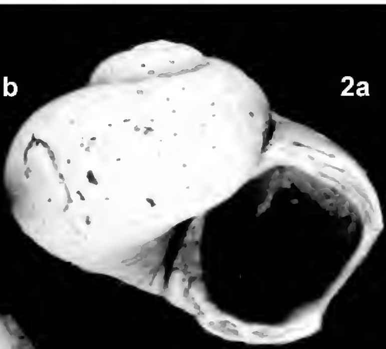
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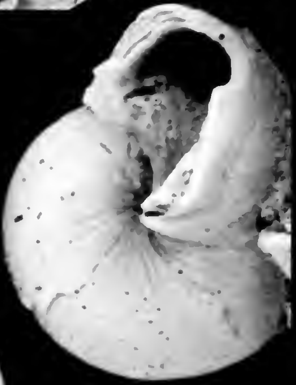
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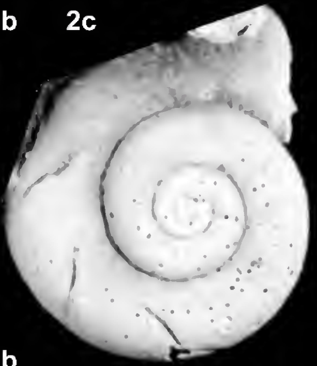
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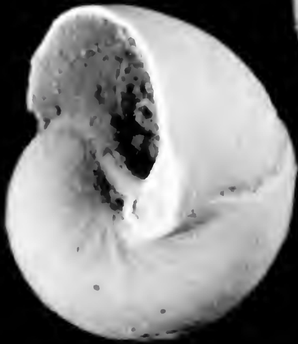
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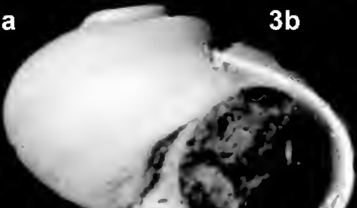
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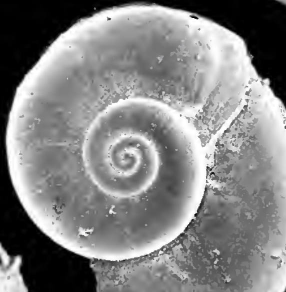
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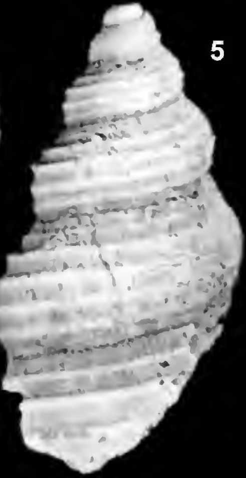
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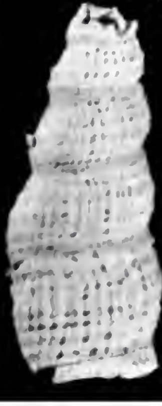
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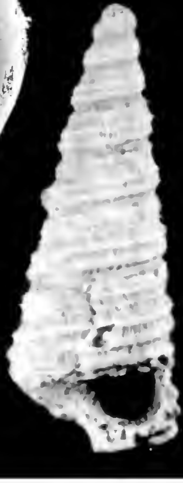
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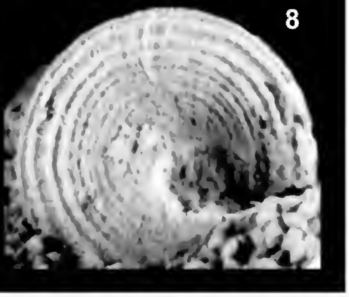
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Primitive termites from the Early Cretaceous of Asia (Isoptera)

Michael S. Engel, David A. Grimaldi & Kumar Krishna

Abstract

New fossil termites (Isoptera) are described and figured from four Early Cretaceous deposits across Asia, including some of the oldest records for the order. In total seven new genera and six new species are established from these sites. A single, alate specimen is documented from the Zaza Formation (Berriasian) of Baissa, Transbaikalia (Siberia, Russia) and is described as *Baissatermes lapideus* n. gen. n. sp. *Baissatermes lapideus* n. gen. n. sp. is the oldest fossil termite presently known and the oldest known example of a social organism. *Valditermes acutipennis* Ponomarenko, from the Aptian of Mongolia, is transferred to a new genus, *Khanitermes* n. gen. (resulting in the new combination, *Khanitermes acutipennis* n. comb.). *Melqartitermes myrrheus* n. gen. n. sp. is described in Neocomian amber from Lebanon. The latest Albian Burmese amber (Myanmar) harbors the greatest diversity of termites hitherto discovered from any Cretaceous amber locality. In total six species are documented in Burmese amber, including the following new taxa and combinations: *Mylacrotermes cordatus* n. gen. n. sp., *Dharmatermes avernalis* n. gen. n. sp., *Proelectrotermes swinhoei* (Cockerell) n. comb., *P. holmgreni* n. sp., *Kachinitermes* n. gen., *Kachinitermes tristis* (Cockerell) n. comb., *Tanytermes anawrahtai* n. gen. n. sp. The significance of these new taxa for understanding early termite evolution and basal relationships within Isoptera is discussed. A checklist of Cretaceous termites is provided.

Keywords: Asia, Isoptera, Mesozoic, paleontology, phylogeny, taxonomy.

Zusammenfassung

Es werden neue fossile Termiten (Isoptera) aus Ablagerungen der frühen Kreide von Asien beschrieben und abgebildet, darunter einige der ältesten Nachweise der Ordnung. Insgesamt werden sieben neue Gattungen und sechs neue Arten eingeführt. Aus der Zaza Formation (Berriasium) von Baissa, Transbaikalien (Sibirien, Russland) wird ein einzelnes, beflügeltes Exemplar als *Baissatermes lapideus* n. gen. n. sp. beschrieben. Es ist die älteste gegenwärtig bekannte fossile Termite und das älteste Beispiel für einen sozialen Organismus. *Valditermes acutipennis* Ponomarenko aus dem Aptium der Mongolei wird einer neuen Gattung, *Khanitermes* n. gen., zugeordnet (das ergibt die neue Kombination *Khanitermes acutipennis* n. comb.). Aus dem Bernstein des Libanon (Neokom) wird *Melqartitermes myrrheus* n. gen. n. sp. beschrieben. Der Burmesische Bernstein (Oberstes Albium; Myanmar) beherbergt die größte Vielfalt an Termiten, die bisher aus einem kreidezeitlichen Bernstein bekannt ist. Insgesamt sind sechs Arten belegt, die die folgenden neuen Taxa und Konbinationen umfassen: *Mylacrotermes cordatus* n. gen. n. sp., *Dharmatermes avernalis* n. gen. n. sp., *Proelectrotermes swinhoei* (Cockerell) n. comb., *P. holmgreni* n. sp., *Kachinitermes* n. gen., *Kachinitermes tri-*

stis (Cockerell) n. comb., *Tanytermes anawrahtai* n. gen. n. sp. Die Bedeutung dieser neuen Taxa für das Verständnis der frühen Evolution der Termiten sowie deren basaler Verwandtschaftsverhältnisse werden diskutiert. Eine Checkliste kreidezeitlicher Termiten wird erstellt.

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1. Introduction

Among the 30 living orders of insects traditionally recognized, termites have singular biological significance. They are the only group of eusocial insects without haplodiploid sex determination, and the only significant group among all insects to feed on wood and other forms of cellulose and lignocellulose. Their diet, in conjunction with advanced sociality, makes termites of pivotal ecological importance. For example, termites process prodigious amounts of wood, grass, humus, dung, and mycelia in the tropical and subtropical regions of the world, and thus have profound effects on the carbon cycling and soils of these regions (reviewed in Grimaldi & Engel 2005). The question of how these insects became so significant is thus not a trivial one.

One approach to addressing the success of termites is historical, specifically based on fossils and phylogenetics. The closest living relative of termites is the relict genus of wood roaches, *Cryptocercus* (e. g., Lo et al. 2000; Grandcolas & D'Haese 2001; Klass & Meier 2006), which is traditionally placed in its own family (e. g., McKittrick 1964) but more recently put in the apparently paraphyletic roach family Polyphagidae (Grandcolas 1996). Though no Jurassic termite has yet been found, Isoptera putatively diverged from a xylophagous "polyphagid" ancestor – one line leading to *Cryptocercus*, the other to termites – in the Late Jurassic, ca. 150–160 mya.

The Mesozoic record of termites (Table 1) was unveiled with the first Cretaceous termite, *Cretatermes*, described 40 years ago (Emerson 1967) from the Late Cretaceous of Labrador. It was not until 14 years later that the second Cretaceous species was reported (Jarzembowski 1981), and by the mid and late 1980's an additional four species became known, three from Europe and one from central Asia (Lacasa-Ruiz & Martínez-Delclòs 1986; Ponomarenko 1988; Schlüter 1989). An additional ten species were described in the 1990's, seven of them from the Early Cretaceous of China (REN 1995). The only other North American Cretaceous termite, *Carinatermes*, was described in 2000 from the Late Cretaceous amber of New Jersey (KRISHNA & GRIMALDI 2000). The only Cretaceous Rhinotermitidae, *Archeorhinotermes*, was described soon thereafter in Burmese amber (KRISHNA & GRIMALDI 2003). To the three species from the Early Cretaceous Crato (Santana) Formation of Brazil (KRISHNA 1990; FONTES & VULCANO 1998) have recently been added reports of a putative six additional species (MARTINS-NETO et al. 2006; BECHLY in press), though the species concepts of the MARTINS-NETO taxa are vague and it is likely some, if not all, will be synonyms.

Herein we describe six new species (some 19% of the known Cretaceous fauna), including the first one in Early Cretaceous Lebanese amber, as well as four additional species from Burmese amber and the oldest known termite fossil (from the Berriasian of Baissa, Transbaikalia, Russia). We also propose three new combinations. As of now Asia (including Central Asia and Asia Minor) has the greatest diversity, with 17 species; in addition, there are nine South American species (all Crato Formation, but which need re-study), four European, and two North American, for a total of 32 species (including the three records of BECHLY (in press)) – a far cry from 40 years ago.

The main purpose of this paper is descriptive, to delineate and figure the new species in detail for a companion study on the phylogeny of living and extinct basal termites (GRIMALDI, ENGEL & KRISHNA in prep.).

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2. Materials and methods

2.1. Material and specimen preparation

All of the specimens considered herein are from the Early Cretaceous of Asia, ranging from the westernmost edges of the continent (in Lebanon), to the Far East in Russia (Siberia) and Mongolia, and to the southern tropics (in northern Myanmar). Compression fossils were studied dry and, at times, with polarized light. Amber pieces were embedded in epoxy following the methods and procedures of NASCIMBENE & SILVERSTEIN (2000) and then trimmed and polished to afford the maximal view of specimen features. Inclusions were then studied using compound and stereomicroscopy. Photomicrographs were prepared using a MicrOptics ML-1000 digital imaging system. Measurements were made for observable features and, therefore, are not entirely consistent across the taxa considered (e. g., the metatibial length was not measureable in all specimens). Type material is located in the following institutions:

AMNH	American Museum of Natural History, New York
NHML	Natural History Museum, London
PIN	Paleontological Institute, Russian Academy of Sciences, Moscow
SEMC	University of Kansas Natural History Museum, Lawrence

2.2. Terminology and descriptions

Morphological terminology in the descriptions is generally that employed widely in isopteran systematics except as noted here. Typically termed "humeral suture", we employ the name "basal cleavage suture" or "basal suture" for the distinctive suture demarcating the apex of the wing scale, where the wings are shed. "Humeral suture" is a misnomer as "humeral" refers to the anterior, i. e., costal, margin of the extreme wing base where there is often in insects a small sclerite called the humeral plate. This anterior basal section of the costal margin, inside the wing scale, is accordingly termed the "humeral margin" herein. The vein CuP is a short, typically arched vein that runs entirely within the wing scale, terminating at, or just before, the posterior edge of the basal suture. This vein is sometimes termed the "claval suture", a misnomer since there is no break made along this vein and while certainly deeply incised it is more appropriately termed the "claval fissure" but is herein referred to strictly as CuP, and as demarcating the anterior and apical margin of the claval area. Lastly, the issue of tarsal reduction is a prominent one in Isoptera. In the basalmost termites the tarsus is pentamerous (i. e., with five articles) but gradually becomes reduced to a tetramerous condition (i. e., with four articles). This reduction results from the gradual minimization of the second tarsal article as is evidenced by the slight reduction of the second article in *Termopsis* relative to the completely pentamerous condition seen in *Mastotermes*. The reduction becomes even more advanced in genera such as *Archotermopsis* in which the metatarsus becomes cryptically pentamerous. In this latter condition the second tarsal article is further reduced such that in dorsal aspect the tarsus appears tetramerous, but the second article is fully visible ventrally demonstrating that it is in fact pentamerous. In its ultimate state, the second tarsal article is lost entirely giving a truly tetramerous tarsus (an even more derived condition seen only in a few Tertiary or modern genera such as *Stylotermes* or *Parastylotermes*, is a trimerous tarsus). However, in order to denote the correct serial homology for this process of reduction we number tarsal articles based on their homologues rather than their physical position in relation to each other. Thus, in tetramerous tarsi the tarsal articles present are the first, third, fourth, and fifth, as accordingly numbered as such (e. g., Figs. 10c–e, 12b).

Nearly all of the genera considered herein are monotypic and we have, therefore, constructed detailed generic descriptions, highlighting characters that are most significant for comparison with modern and other fossil termite genera as presently defined. Specific descriptions are, accordingly, abbreviated and may need to incorporate features presently considered "generic" should additional species be discovered that can be readily included with slight modification of the generic diagnosis. Taxa are purposefully not assigned to higher categories (i. e., families) pending an on-going phylogenetic study of basal living and fossil termites designed to redefine the families and subfamilies of Isoptera (Grimaldi, Engel & Krishna in prep.). Recent assertions to place termites as a single family within Blattaria (Inward et al. 2007) are without merit and do nothing to provide nomenclatural stability. The placement of termites among roaches has been known for nearly a century and they had even been considered a suborder of Dictyoptera at times in the past (e.g., McKittrick 1964). The Isoptera could be easily once again considered a suborder or infraorder within Blattaria without altering the internal classification of termites and immediately eliminating the paraphyly of Blattaria (Lo et al. 2007), or the latter could be segregated into multiple orders. The application of the ordinal rank is merely semantic and serves only to indicate relative degrees of inclusiveness of a particular taxon in relation to other taxa. Regardless, the Isoptera are herein rightfully retained as a distinct, multi-familial lineage of the Dictyoptera.

3. Systematic Paleontology

3.1. Zaza Formation, Russia

Baissa is widely considered one of, if not the, most important Early Cretaceous localities for compression fossils of insects. The fidelity of preservation is relatively high and the fauna is remarkably diverse, with many species being outright abundant. To date, more than 10,000 fossil insects have been recovered by the scientists of the Paleontological Institute's Arthropoda Laboratory (Rasnitsyn & Quicke 2002). The locality is composed of marls and limestones in the Zaza Formation (Rasnitsyn & Quicke 2002) of approximately Berriasian age (Rasnitsyn et al. 1998). Baissa is located along the Vitim River in Central Siberia (western Transbaikalia).

Genus *Baissatermes* n. gen.

Type species: *Baissatermes lapideus* n. gen. n. sp.
Etymology: The new genus-group name is a combination of the locality Baissa (from which the fossil originates) and *Termes*, the oldest generic name in Isoptera. The name is masculine.

Diagnosis. – Imago. Head robust; Y-shaped coronal ecdysial cleavage line faintly visible; right mandibular apex evident, with two, pointed marginal teeth, first marginal tooth about as long as apical tooth; subsidiary tooth absent. Pronotum large, anterior margin apparently slightly emarginate, lateral border straight, parallel with longitudinal axis of body. Wings with well-defined basal suture (Figs. 1, 2b, c); forewing narrow, with rounded apex; forewing scale with basal suture weakly convex, with veins apparently originating inside scale; Sc short, terminating on anterior wing margin shortly after basal suture; R simple and short, terminating at basal third of wing length; Rs extending to wing apex and gradually broadening radial field toward apex such that Rs branches encompass anterior wing apex, with about seven main branches evident, some apically with minute, secondary branches along anterior wing margin; M running about equidistant from Rs and CuA, branches of M not well preserved, with at least some evidence of dichotomous branching in distal half of wing length, apparently terminating just posterior of wing apex and with posteriormost branch terminating on posterior wing margin at point one-third of wing

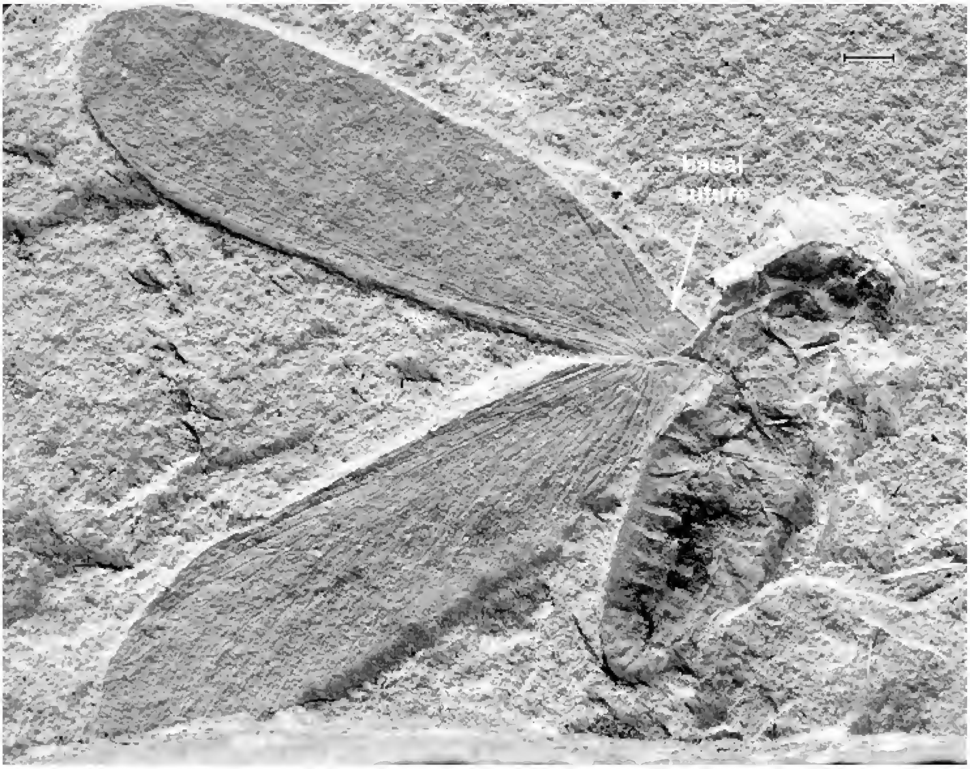

Fig. 1. Photomicrograph of holotype imago of *Baissatermes lapideus* n. gen. n. sp. (PIN 3064/8583); Zaza Formation, Berriasian; Baissa, Russia. – Scale bar = 1 mm.

length from apex; CuA pectinately branched, terminating on posterior wing margin at about two-thirds wing length.

Comments. – Although preserved such that relatively few characters can be gleaned from the single specimen, the significance of *Baissatermes lapideus* n. gen. n. sp. is its age. The Baissa locality dates from the Berriasian (vide supra), making this the oldest record of a termite yet documented and the oldest evidence of a eusocial organism. Previously *Meiatermes bertrani* LACASA-RUIZ & MARTÍNEZ-DELCLÒS (1986), from the important Montsec locality in Spain, was believed to be the oldest termite and social insect (MARTÍNEZ-DELCLÒS & MARTINELL 1995), but these deposits are of Early Barremian age (ANSORGE 1993; MARTÍN-CLOSAS & LÓPEZ-MORÓN 1995), not Berriasian-Valanginian.

Baissatermes lapideus n. gen. n. sp.
Figs. 1, 2b, c

2002 Hodotermitid sp. – RASNITSYN & QUICKE, p. 272, fig. 380.

Holotype: Imago, PIN 3064/8583 (Fig. 1).
Stratum typicum: Zaza Formation, Berriasian.

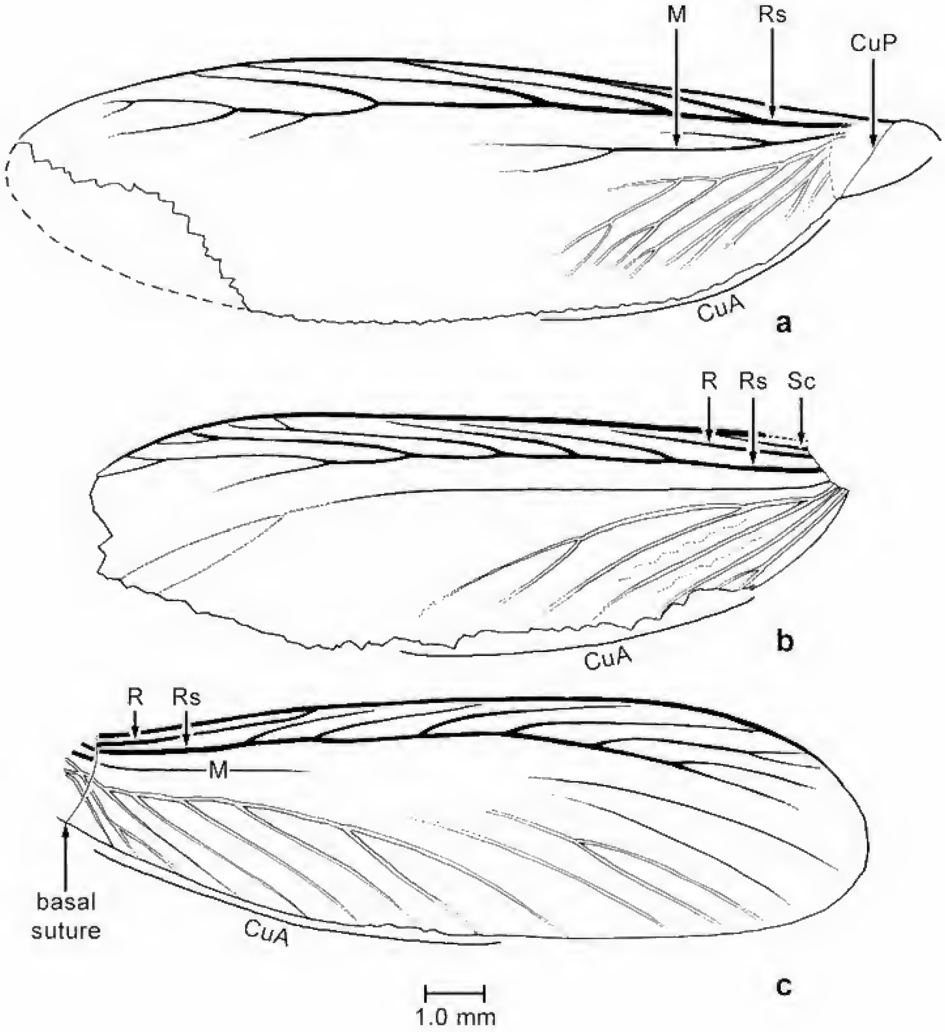

Fig. 2. Wing venation of compression fossil termites from the Early Cretaceous of Mongolia and Siberia. **a**: Forewing venation of holotype of *Khanitermes acutipennis* (PONOMARENKO) n. comb. (PIN 4271/1); Shar-Tologoy Formation, Early Cretaceous; Shar-Tologoy, Mongolia. **b–c**: Holotype of *Baissatermes lapideus* n. gen. n. sp. (PIN 3064/8583); Zaza Formation, Berriasian; Baissa, Transbaikalia, Russia. **b**: Discernible left forewing venation. **c**: Discernible details of right forewing venation.

Locus typicus: Baissa, Transbaikalia.

Etymology: The specific epithet is the Latin word lapideus, meaning "of stone".

Diagnosis. – As for the genus (vide supra).

Description. – Imago. Head length 2.2 mm, width 2.1 mm; median pronotum length 1.0 mm. Length of forewing from basal suture to apex 12.7 mm; forewing width 4.0 mm; length of hind wing from basal suture 13.1 mm; hind wing width 3.7 mm; forewing with Sc, R, and Rs more distinctly sclerotized than M and CuA; Sc relatively short, terminating on anterior wing margin in basal quarter of wing not far from basal suture; R simple and short, terminating on anterior wing margin in basal third of wing just beyond termination of Sc; Rs running relatively parallel to anterior wing margin until about wing midlength, then gently curving posteriorly toward wing apex, with six branches, more apical branches with short, secondary branches along wing margin; M relatively simple, apparently branching beyond wing midlength, curving slightly toward posterior wing margin, total number of branches indeterminate, medial field just posterior of wing apex and ending in apical third of wing; CuA pectinately branched, branches simple except one basal branch with short secondary fork, cubital field encompassing nearly basal two-thirds of posterior wing margin.

3.2. Shar-Tologoy Formation, Mongolia

The Mesozoic deposits of Mongolia have proven to be a great source of Early Cretaceous insects (reviewed in RASNITSYN & QUICKE 2002). The Shar-Tologoy Formation, in particular, has yielded a wealth of species in diverse orders such as Ephemeroptera (e. g., the giant mayfly *Ephemeropsis melanurus* COCKERELL), Odonata, Orthoptera, Hemiptera, Neuroptera, Coleoptera, Diptera (e. g., *Prospeolepta brevicubita* BLAGODEROV), and Trichoptera. A single termite has also been described from the Aptian-aged Shar-Tologoy locality (PONOMARENKO 1988), and we herewith take the opportunity to provide new information on this species.

Genus *Khanitermes* n. gen.

Type species: *Valditermes acutipennis* PONOMARENKO, 1988.

Etymology: The new genus-group name is a combination of Khan, the title of political and military leaders in the ancient Mongol Empire, and *Termes* (meaning, "termite"), the first generic name of the Isoptera. The generic name is a reference to the most famous Khan of ancient Mongolia, GENGHIS KHAN (c. 1162–18 August 1227, born BORJIGIN TEMÜJIN, the former being his surname, was bestowed with the title Khan and became GENGHIS KHAN in 1206). He united the Mongol Tribes into the Mongol Empire in 1206. The name is masculine.

Diagnosis. – Imago. Forewing narrow, with rounded apex (not acutely pointed as indicated by the original description and the specific epithet); forewing scale with basal suture gently convex, with veins apparently originating inside of forewing scale; CuP relatively straight, not forming a distinct, convex arch (Fig. 2a); R not evident as basal anterior margin of wing apparently folded; Rs with pectinate branches extending anteriorly, those branches in apical third of wing with some secondary branches, first branch originating in basal quarter of forewing not far beyond basal suture, Rs relatively straight along its course (not curved posteriorly), although not parallel with costal margin of wing and ultimately terminating at wing apex in more posterior position (thus radial field widens toward wing apex) (Fig. 2a); M running about equidistant from Rs and Cu; M dichotomously branching, with apparent total of four branches, although small stub of possible fifth, basal, anteriorly-directed branch apparently present (this branch appears in basal quarter of forewing and not far beyond basal suture), first distinct branching of M at basal third of forewing length, next branching apparently near forewing midlength; Cu apparently terminating just beyond forewing midlength, with various branches and some secondary branches; CuP straight, demarcating an apically-pointed claval area (Fig. 2a).

Comments. – PONOMARENKO (1988) placed his Early Aptian fossil in the genus *Valditermes*, a group previously known only from a single Hauterivian species from England (JARZEMBOWSKI 1981). Two of us (M. S. E. and D. A. G.) were afforded the opportunity to study PONOMARENKO's holotype in Moscow in late July 2002 and the new figure of the wing venation is based upon observations and notes taken at that time (Fig. 2a). While the wing is relatively narrow, the apex is not as truly pointed as indicated by PONOMARENKO's (1988) original reconstruction. Instead, the more posterior portions of the forewing apex are simply not preserved, giving those surviving components a rather apically acute appearance.

Notable differences between the Mongolian (Shar-Tologoy) species (*Khanitermes* n. gen.) and the British (Lower Weald Clay) species *(Valditermes)* include: Rs extending to wing apex and slightly toward posterior but overall relatively straight along its course and not distinctly curved posteriorly (Rs distinctly, albeit gently, curving posteriorly in apical third of wing in *Valditermes*); and M with dichotomous branching, apparently with maximally four branches (M pectinate in *Valditermes*).

Khanitermes acutipennis (PONOMARENKO) n. comb.

Fig. 2a

1988	*Valditermes acutipennis* PONOMARENKO, sp. nov. – PONOMARENKO, p. 71, table 13, fig. 1.
1991	*Valditermes acutipennis* PONOMARENKO. – JARZEMBOWSKI, p. 93.
1993	*Valditermes acutipennis* PONOMARENKO, 1988. – NEL & PAICHELER, p. 136.
1995	*Valditermes acutipennis.* – MARTÍNEZ-DELCLÒS & MARTINELL, p. 595.
2000	*Valditermes acutipennis.* – KRISHNA & GRIMALDI, p. 133.
2000	*Valditermes acutipennis* PONOMARENKO. – THORNE et al., p. 81, 85, fig. 2.
2005	*Valditermes acutipennis.* – GRIMALDI & ENGEL, p. 250.
2006	*Valditermes acutipennis* PONOMARENKO. – MARTINS-NETO et al., p. 125.

Holotype: Imago, PIN 4271/1.

Stratum typicum: Bon-Tsagan Group, Shar-Tologoy Formation, Early Cretaceous, Aptian.

Locus typicus: Mongolia, Bayan Khongor District, Gobi Altai, 33 km North Bayan-Leg area, Shar-Tologoy.

Diagnosis. – As for the genus (vide supra).

3.3. Amber from Lebanon

The Neocomian amber from various localities in Lebanon represents the oldest amber with macroscopic biological inclusions. The diversity of taxa preserved in Lebanese amber is remarkable, with thousands of inclusions representing 13 insect orders (not including the order Isoptera, newly reported herein), as well as various arachnids, feathers, and even a lizard. Here we describe the first termite from Lebanese amber (Fig. 3), although the precise outcrop in Lebanon from which this specimen originated is unknown.

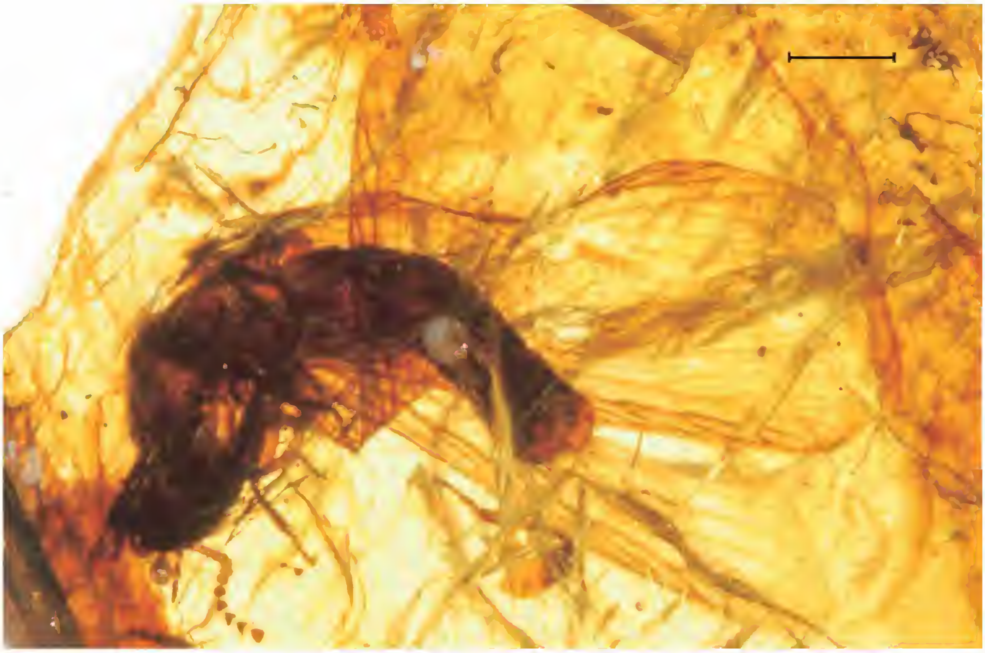

Fig. 3. Photomicrograph of holotype imago of *Melqartitermes myrrheus* n. gen. n. sp. (AMNH L-Iso1); Lebanese amber; Neocomian. – Scale bar = 1 mm.

Genus *Melqartitermes* n. gen.

Type species: *Melqartitermes myrrheus* n. gen. n. sp.

Etymology: The new genus group name is a combination of the Phoenician name MELQART and *Termes* (meaning, "termite"), the first generic name of the Isoptera. MELQART (also known as MELKURT), son of BAAL, was the Phoenician god of the underworld and patron of ancient Tyre, the city famously besieged and conquered by ALEXANDER THE GREAT in 332 B. C. when his request to make sacrifice to MELQART was denied by the Tyrians. The name is masculine.

Diagnosis. – Imago. Head robust (Fig. 3, 4a), posterior border faintly curved, lateral borders parallel-sided; right mandible (as seen ventrally) with at least two marginal teeth (Fig. 4a), each tooth about as long as apical tooth, subsidiary tooth not present; antenna moniliform, with at least 13 articles (total article number unknown), flagellar articles progressively larger from base to preserved apex; compound eyes without anterior emargination, apparently circular, separated from lower margin of head by less than eye diameter, separated from posterior border of head by about eye diameter or slightly less; ocelli absent; fontanelle apparently absent; ventral cervical sclerite present (Fig. 4a), sclerite transverse, narrowly rectangular, with faint medial depression and scattered minute setae. Pronotum large, flat, and broad, slightly broader than head; anterior border weakly concave; lateral borders apparently parallel-sided, with posterior corners gently rounded inward; posterior border straight, thus pronotum with a largely quadrate shape. Procoxa apparently without ventral keel or carina; femora apparently not carinate or keeled ventrally; all

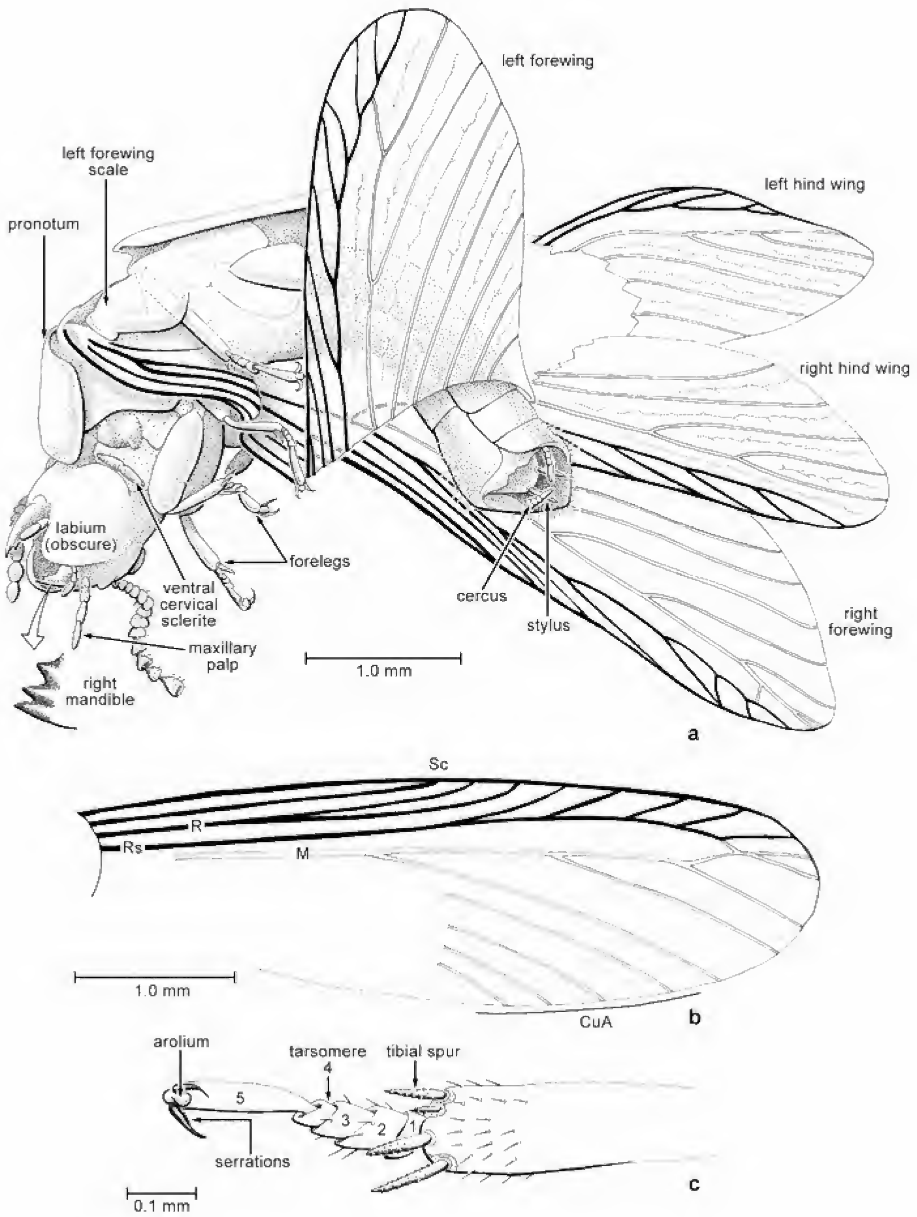
left forewing
left forewing scale
pronotum
left hind wing
right hind wing
labium (obscure)
forelegs
ventral cervical sclerite
maxillary palp
right mandible
cercus
stylus
right forewing
1.0 mm
a
Sc
R
Rs
M
1.0 mm
CuA
b
arolium
tarsomere 4
tibial spur
5
3
2
1
serrations
0.1 mm
c

Fig. 4. Holotype imago of *Melqartitermes myrrheus* n. gen. n. sp. (AMNH L-Iso1); Lebanese amber; Neocomian. **a**: Lateral habitus. **b**: Reconstruction of visible portions of forewing venation. **c**: Metatarsus, metapretarsus, and apex of metatibia.

tarsi completely pentamerous (Fig. 4c); tibial spur formula 3-4-4, spurs of all legs serrated; large arolium present on all legs (Fig. 4c), pretarsal ungues with minute, apical serrations along inner margin. Wings largely hyaline, slightly infuscate on membrane; membrane not reticulate, although with some more faintly infuscate lines apically between longitudinal veins. Forewing veins Sc, R, and Rs heavily pigmented, remainder lightly pigmented (Fig. 4b); forewing scale large, overlapping hind wing base, humeral margin weakly convex, basal suture convex; all veins originating inside wing scale; Sc and R elongate, Sc terminating on costal margin just prior to wing midlength, R forking in basal third of wing, with branches terminating at wing midlength and slightly beyond wing midlength, respectively; Rs with 5–6 anterior branches, first branch arising beyond wing midlength; Rs running generally parallel to costal wing margin for entire length, near wing apex connecting to anteriormost branch of M; radial field relatively narrow for entire length of wing; visible portion of M with five long, pectinate branches gently curved toward posterior margin, apicalmost branch connected to apicalmost branch of Rs and terminating at wing apex, first branch of M apparently arising at forewing midlength; hind wing without anal lobe. Abdomen relatively narrow, cylindrical (Fig. 4a), sides generally parallel; cerci well developed (Fig. 4a), apparently six-segmented; styli present (Fig. 4a), length slightly more than one-half length of cercus.

Comments. – *Melqartitermes* n. gen. has many notable plesiomorphic features including the presence of the ventral cervical sclerite (absent in all Isoptera except *Mylacrotermes* n. gen., vide infra); fully pentamerous tarsi in which the second tarsomere is neither reduced nor partially obscured when viewed from above (in genera such as *Archotermopsis*, *Hodotermopsis*, and *Zootermopsis* the tarsus is cryptically pentamerous, appearing tetramerous when viewed from above); the presence of a large arolium; the serrated edges to the spurs; the large forewing scale; the large and relatively flat pronotum (i. e., not bowed transversely and saddle-shaped in profile); the long, multi-segmented cerci, and the presence of styli. Definitive assignment of this fossil to family and/or subfamily awaits the completion of presently ongoing phylogenetic studies combining neontological and paleontological material. However, comments can be made on some features of *Melqartitermes* n. gen. and their distribution among the higher lineages of basal Isoptera as they are presently defined.

The presence of the ventral cervical sclerite, fully pentamerous tarsi, multi-segmented cerci, serrated spurs, and a large arolium attest to the primitive nature of this fossil. Nonetheless, the absence of an anal lobe in the hind wing is a peculiar apomorphy of *Melqartitermes* n. gen. In the current system of the Isoptera (e. g., as outlined by Engel & Krishna 2004), this genus might most closely approximate *Stolotermes* and *Porotermes* or *Hodotermes* and *Anacanthotermes*, particularly the former two owing to the narrow radial field, with Rs generally parallel to the costal margin. However, *Melqartitermes* n. gen. differs from all of these in its large pronotum with a straight anterior border and the presence of the ventral cervical sclerite, and from the latter two in the completely pentamerous tarsi and narrow radial field. The genus *Archotermopsis* has an apical mandibular structure and venation that perhaps most resembles those of *Melqartitermes* n. gen., although significant differences remain between these genera.

As noted, *Melqartitermes* n. gen. has a narrow radial field along the entire anterior margin of the forewing, with Rs not branching extensively near the wing apex but instead simply joining the anteriormost branch of M near the wing apex. This differs notably from other primitive Cretaceous fossils such as *Carinatermes* and *Meiatermes*, as well as the Tertiary fossil genus *Ulmeriella*, all of which have fully pentamerous tarsi. In addition, *Melqartitermes* n. gen. differs from *Carinatermes* in the presence of arolia (absent in *Carinatermes*), a pronotum with a straight anterior margin (deeply concave in *Carinatermes*), and the humeral border of its forewing scale weakly convex (straight in *Carinatermes*). From *Meiatermes* the new genus further differs by the longer Sc and R, with Sc extending to about the forewing midlength (both terminating before the forewing midlength in *Meiatermes*), and the more extensively branched M.

The absence of the fontanelle and the procoxal keel is somewhat uncertain as both of these surfaces are exceedingly difficult to see owing to the nature of preservation of the holotype of the type species.

Melqartitermes myrrheus n. gen. n. sp.

Figs. 3, 4

Holotype: Imago (Fig. 3), AMNH L-Iso1.
Age: Early Cretaceous, Neocomian.
Locus typicus: Lebanon.
Etymology: The specific epithet is a reference to myrrh, an aromatic gum-resin exuded by *Commiphora abyssinica* (O. Berg.) Engl. (Burseraceae) and related species, and used in trade by the ancient people of the Mediterranean.

Diagnosis. – As for the genus (vide supra).

Description. – As described for the genus with the following additions: Imago. Width of head 0.82 mm; compound eye diameter 0.29 mm; lateral length of pronotum 0.82 mm; length of forewing from basal suture to apex 4.6 mm; width of forewing 1.38 mm; length of forewing scale 0.74 mm; width of hind wing 1.38 mm. Integument dark brown and (where evident) faintly imbricate; setation not evident except on ventral cervical sclerite and pleura, setae short, simple, and anteriorly- or laterally-directed. Forewing with R branched near its midlength; Rs terminating just slightly before wing apex, with five branches, apically joined to M by rs-m just before midlength of apicalmost branch; M terminating at wing apex, with at least five main branches evident, all branches simple, basalmost branch terminating at apical fifth of wing along posterior wing margin; only four apical branches of CuA visible, all apparently simple, cubital field apparently occupying about three-quarters of posterior wing margin.

3.4. Amber from Myanmar

While long believed to be of Tertiary age, amber from northeastern Burma was recently and correctly revealed to be Early Cretaceous in age, dating from the latest Albian (Grimaldi et al. 2002; Cruickshank & Ko 2003). The fauna is remarkably diverse, perhaps more so than any other Cretaceous amber assemblage. Concomitantly, the termite fauna of Burmese amber is similarly important, representing the most diverse Cretaceous amber assemblage of Isoptera. Two species have been documented (Cockerell 1916, 1917; Williams 1968), to which we here add a further four (Figs. 5–12).

Genus *Mylacrotermes* n. gen.

Type species: *Mylacrotermes cordatus* n. gen. n. sp.
Etymology: The new genus-group name is a combination of *Mylacris* (meaning, "roach") and *Termes* (meaning, "termite"). The name is masculine.

Diagnosis. – Imago. Head rounded, lateral and posterior margins gently rounded; antenna filiform basally with articles becoming more moniliform apically, with 14 articles; compound eyes circular, relatively small (Fig. 5a), separated from lower margin of head by apparently less than diameter, separated from posterior border of head by about 2.75 times diameter; ocelli absent; fontanelle absent; occipital carina present (Fig. 5b); single, well-sclerotized, ventral cervical sclerite present (Fig. 5b), sclerite large and roughly U-shaped; lateral cervical sclerites elongate, apparently without longitudinal groove. Pronotum large, slightly wider than head (Figs. 5a, b), cordate (Fig. 5a) (i. e., anterior margin deeply concave, lateral borders converging posteriorly, posterior margin rounded). Tibial spur formula 2-2-3 (two spurs on midleg, with a closely approximated subapical spine that appears as a third spur), with a single subapical spine on inner surface of meso- and metatibia (Figs. 5d, e), spurs minutely serrated; tarsi completely pentamerous (Figs. 5d, e); arolium absent. Wings not preserved except for bases; forewing scale very large, apparently without defined basal suture or well-defined scales (i. e., wings roughly torn when shed), all veins originating in wing scale; venation at wing base distinctly corrugated (Fig. 5a); humeral margin broadly arched and costal area broad (Fig. 5a); membrane of scale relatively well-sclerotized (i. e., tegminous), with distinct reticulations posterior to CuA (Fig. 5a); termination of CuP (claval fissure) on posterior wing margin distinctly basal to and separated from apical margin of wing scale; hind wing without defined basal suture, margin roughly torn (as in modern *Mastotermes darwiniensis* FROGGATT). Cerci long (Fig. 5c), surpassing apex of abdomen; segmentation not visible.

Comments. – *Mylacrotermes* n. gen. is, along with *Melqartitermes* n. gen. (vide supra), one of the most primitive known termites, exhibiting some clearly roach-like features such as the presence of ventral cervical sclerites as well as notable plesiomorphies for the Isoptera. Like *Mastotermes* the new genus has completely pentamerous tarsi on all legs, a well-defined occipital carina, a strong procoxal carina (i. e., "keeled procoxae"), a relatively well-sclerotized wing base with reticulations present posterior to CuA, a relatively broad costal area in the wing base, a broadly arched humeral margin to the wing base, a broad pronotum, and long cerci. Unlike *Mastotermes*, however, *Mylacrotermes* n. gen. lacks an arolium, lacks a basal cleavage suture in the forewing, and primitively retains a ventral cervical sclerite and corrugated wing veins. We can only presume that *Mylacrotermes* n. gen. would also have primitively retained a large anal lobe or fan in the hind wing owing to its presumed position as basal relative to *Mastotermes*.

Mylacrotermes cordatus n. gen. n. sp.

Figs. 5–6

Holotype: Imago (dealate) (Fig. 6), SEMC KU-Bu-045.
Age: Early Cretaceous, latest Albian.

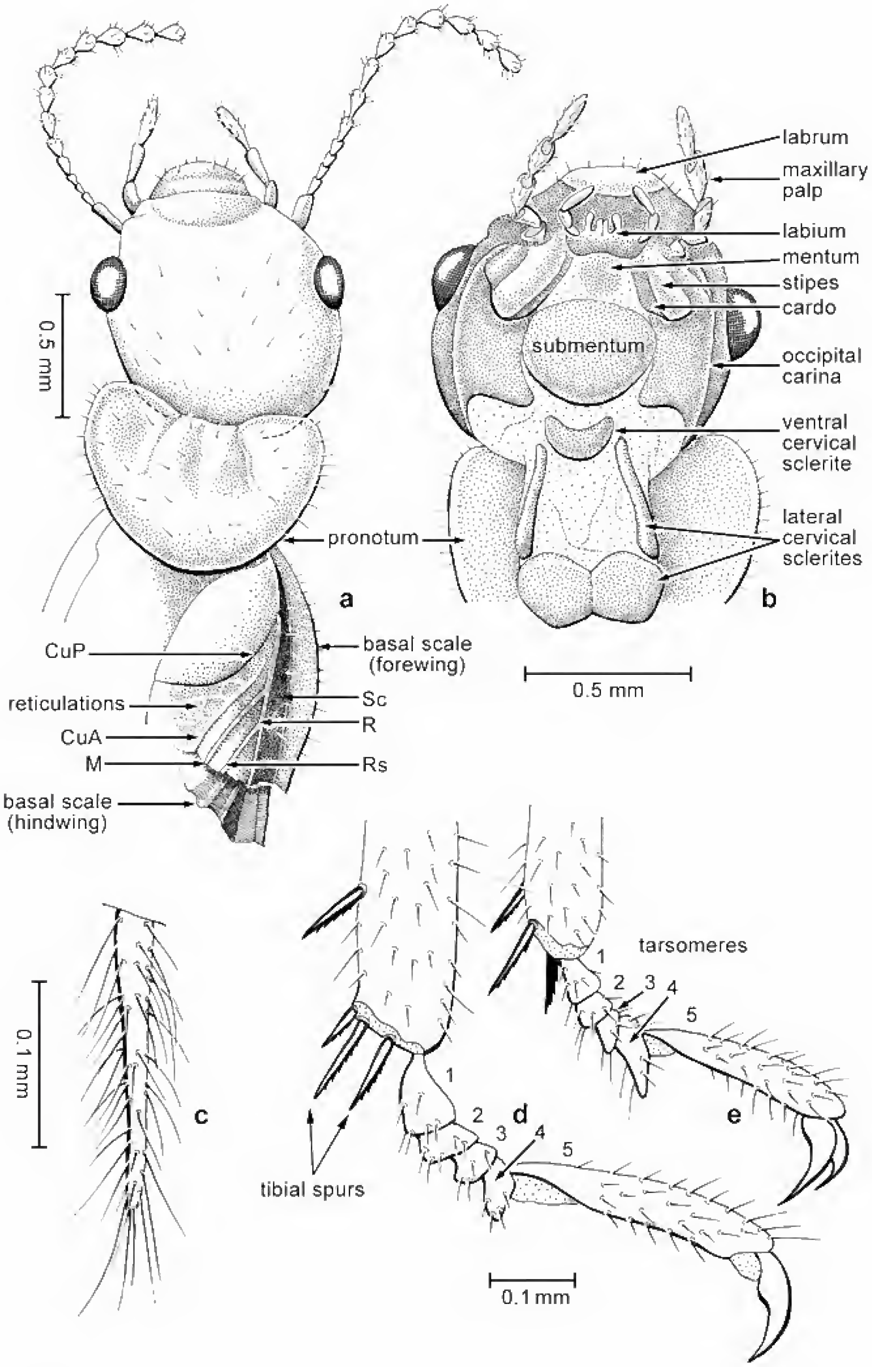
0.5 mm
pronotum
a
CuP
reticulations
CuA
M
basal scale (hindwing)
basal scale (forewing)
Sc
R
Rs
labrum
maxillary palp
labium
mentum
stipes
cardo
submentum
occipital carina
ventral cervical sclerite
lateral cervical sclerites
b
0.5 mm
0.1 mm
c
tibial spurs
1
2
3
4
5
d
0.1 mm
tarsomeres
1
2
3
4
5
e

Fig. 5. Holotype imago of *Mylacrotermes cordatus* n. gen. n. sp. (SEMC KU Bu-045); Burmese amber, latest Albian; Tanai Village, Myanmar. **a**: Detail of head (dorsal aspect), prothorax, and wing bases. **b**: Detail of head and anterior prothorax (ventral aspect). **c**: Cercus. **d**: Metatarsus, metapretarsus, and apex of metatibia. **e**: Mesotarsus, mesopretarsus, and apex of mesotibia.

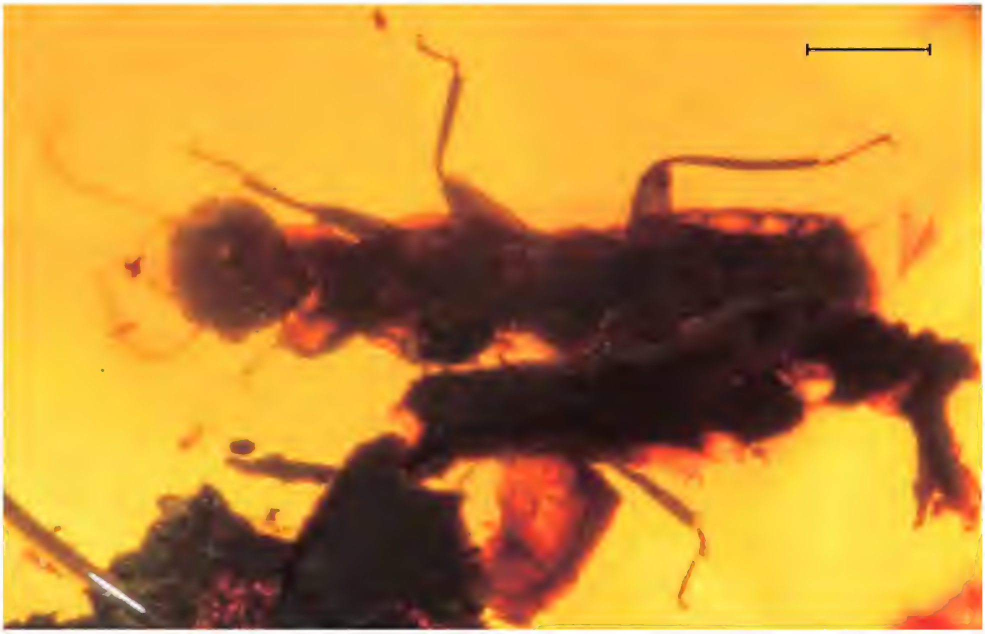

Fig. 6. Photomicrograph of holotype imago of *Mylacrotermes cordatus* n. gen. n. sp. (KU Bu-045); Burmese amber, latest Albian; Tanai Village, Myanmar. – Scale bar = 1 mm.

Locus typicus: Myanmar (Burma), Kachin, Tanai Village (on Ledo Road 105 km NW Myitkyna).

Etymology: The specific epithet is the Latin term cordatus (meaning "heart-shaped") and refers to the heart-shaped pronotum, characteristic of the species.

Diagnosis. – As for the genus (vide supra).

Description. – Imago (dealate). Length of head to apex of labrum 1.28 mm; approximate width of head 1.02 mm; compound eye diameter 0.33 mm; maximum length of pronotum 0.74 mm; length of pronotum along midline 0.62 mm; length of metatibia 1.07 mm; length of forewing scale 0.97 mm. Integument dark brown except ventrally on legs, cervix, and thorax brown, apparently faintly imbricate. Head and pronotum with scattered, erect, simple setae, those on lateral margins of pronotum slightly longer and more prominent; setae of remainder of thorax and abdomen slightly shorter and more sparse except at apex of abdomen setae slightly longer than those of pronotum and more dense than elsewhere on body; short, erect, simple setae along humeral margin of wing scale but not evident on surface of scale; cerci with numerous, elongate, simple, apically-directed, suberect setae.

Genus *Dharmatermes* n. gen.

Type species: *Dharmatermes avernalis* n. gen. n. sp.

Etymology: The new genus-group name is a reference to the Dharmic faiths (the principal Dharmic faiths being Hinduism, Buddhism, Jainism, and Sikhism) predominant in Myanmar and surrounding countries. The name is, accordingly, a combination of Dharma and *Termes*, the oldest generic name in Isoptera. The name is masculine.

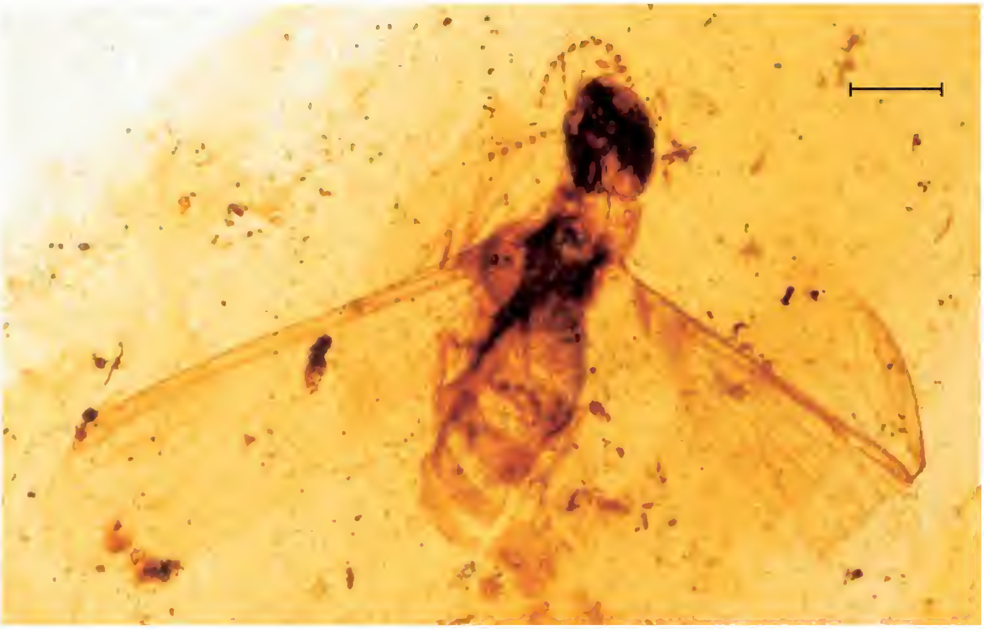

Fig. 7. Photomicrograph of holotype imago of *Dharmatermes avernalis* n. gen. n. sp. (AMNH Bu-313); Burmese amber, latest Albian; Tanai Village, Myanmar. – Scale bar = 1 mm.

Diagnosis. – Imago. Head broader than long, roughly rectangular, lateral borders parallel, posterior border gently rounded (Fig. 7); left mandible (as seen ventrally) with at least two, sharply-pointed marginal teeth (Fig. 8a), each tooth shorter than apical tooth, subsidiary tooth not present; lacinia with inner margin fringed with setae (Fig. 8a), possibly with two teeth (a smaller, subapical one) but this is obscure; molar edge of right mandible serrate (Fig. 8a) (as seen in shadowed profile; serrations likely corresponding to transverse ridges running across molar surface); antenna moniliform, with at least 14 articles (total article number unknown), basal articles smaller and ring-like; compound eyes circular, apparently separated from lower margin of head by less than one-half compound eye diameter, separated from posterior border of head by about 2.25 times compound eye diameter; ocelli absent; fontanelle absent. Pronotum large, flat, and broad, slightly broader than head; anterior border almost straight to weakly convex; lateral borders apparently parallel-sided, with posterior corners gently rounded inward; posterior border straight, thus pronotum with a largely quadrate shape. Metatibia with four spurs, spurs minutely serrated, metatibia without subpical spines; tarsi apparently pentamerous; pretarsus with arolium apparently present (Fig. 8b). Wings hyaline, membrane not reticulate; basal suture very weakly curved, nearly straight; CuP (claval fissure) similarly nearly straight, terminating slightly basad posterior point of termination of basal suture; diagnosis of venation based on right forewing (Fig. 8d) (vide Comments, infra); veins Sc, R, and Rs heavily pigmented, remainder lightly pigmented; forewing scale large, overlapping hind wing base, humeral margin almost straight (Fig. 8e), basal suture nearly straight (Fig. 8e); all veins originating inside wing scale (Fig. 8e); Sc short, terminating on costal margin in basal fifth of wing; R simple and short, terminating in

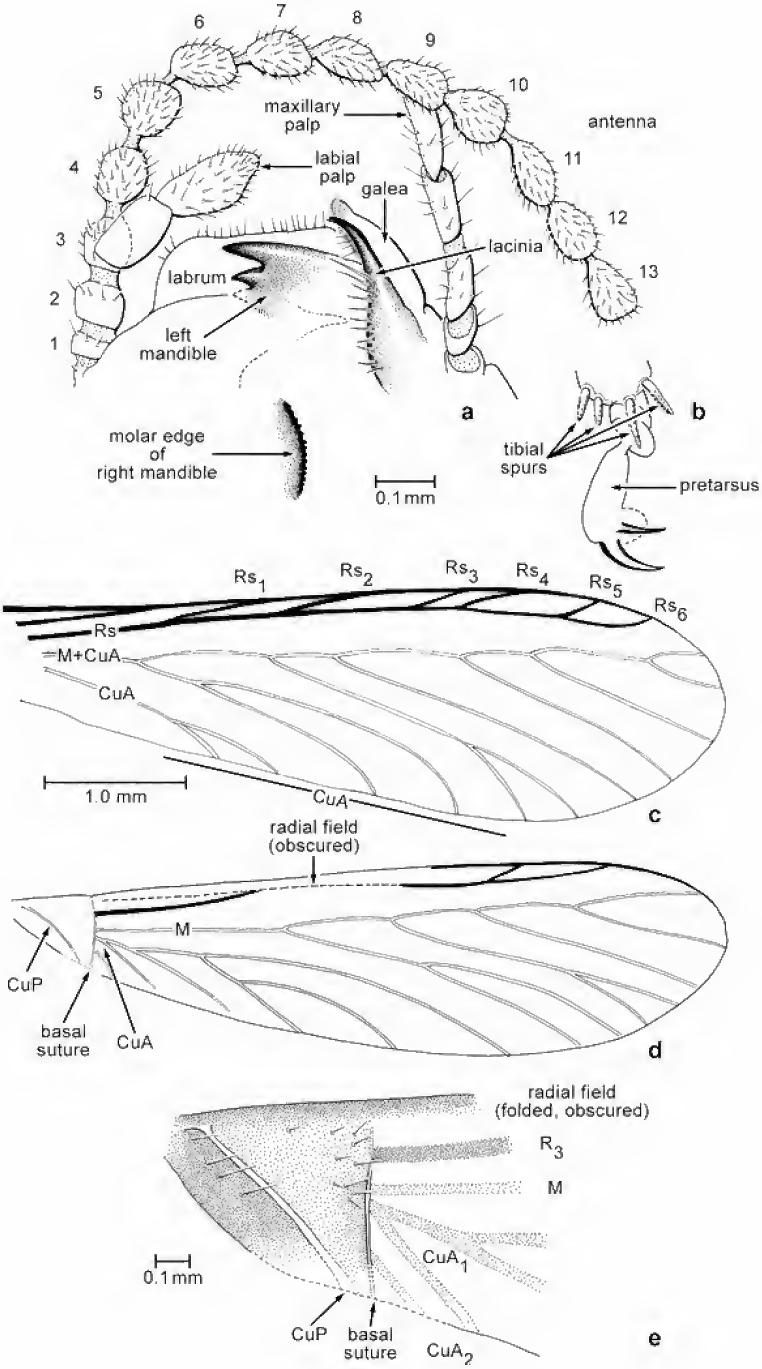
6
7
8
9
5
10
maxillary palp
antenna
4
labial palp
11
galea
12
3
lacinia
labrum
13
2
1
left mandible
a
molar edge of right mandible
0.1 mm
tibial spurs
b
pretarsus
Rs$_1$
Rs$_2$
Rs$_3$
Rs$_4$
Rs$_5$
Rs$_6$
Rs
M+CuA
CuA
1.0 mm
CuA
c
radial field (obscured)
M
CuP
basal suture
CuA
d
radial field (folded, obscured)
R$_3$
M
CuA$_1$
0.1 mm
CuP
basal suture
CuA$_2$
e

Fig. 8. Holotype imago of *Dharmatermes avernalis* n. gen. n. sp. (AMNH Bu-313); Burmese amber, latest Albian; Tanai Village, Myanmar. **a**: Anteriormost portion of head (ventral aspect). **b**: Metatarsus, metapretarsus, and extreme apex of metatibia (as preserved). **c**: Left forewing venation (teratological: vide text). **d**: Right forewing venation. **e**: Right forewing base.

basal quarter of wing; Rs with six anterior branches, first branch arising at basal third of wing; Rs running parallel to costal wing margin for entire length; radial field relatively narrow for entire length of wing (as in Termopsidae); M with long, pectinate branches, branches relatively straight and angled toward posterior margin except basalmost branches slightly and gently curved, first branch of M arising before forewing midlength, medial field encompassing wing apex; apicalmost branch of CuA terminating on posterior wing margin just before apical third of forewing length; hind wing without anal lobe; hind wing broader than forewing (likely teratological: vide Comments, infra). Apical segments of abdomen damaged.

Comments. – The venations of the two forewings in the holotype of *Dharmatermes avernalis* n. gen. n. sp. exhibit striking differences (cf. Figs. 8c, d), clearly resulting from a teratology in the formation of the left forewing (Fig. 8c). The right forewing depicts a more typical venation (Fig. 8d), with the stems of M and CuA separate at the basal suture. In the left forewing, however, M and CuA are partially fused, resulting in a composite venation whereby the more apical branches of CuA appear as a basal, forked branch of M. A nearly identical form of teratological fusion of M and CuA is seen in modern termites. For example, individuals of the kalotermitid *Neotermes fletcheri* HOLMGREN & HOLMGREN are known to sometimes have M and CuA partially fused, giving rise to the same condition in which the basal, forked branch or branches of "M" are actually the more apical branches of CuA (e. g., ROONWAL & SEN-SARMA 1960). Interestingly, in the formation of this teratology the hind wing is correspondingly broadened such that the wings are no longer homonomous, similar to the condition seen in the holotype of *D. avernalis* n. gen. n. sp.

The right forewing venation of *Dharmatermes* n. gen. (Fig. 8d) is not without similarity to that of *Stolotermes* and *Porotermes* (vide etiam *Tanytermes* n. gen., infra). All three genera have a narrow radial field running parallel to the anterior wing margin.

The tarsi are apparently pentamerous and the pretarsi apparently bear an arolium but these are difficult to discern owing to incomplete preservation of the holotype and these features should be considered tentative. In addition, it was not possible to determine the spur number of the pro- and mesotibia as these legs are damaged in the holotype.

Dharmatermes avernalis n. gen. n. sp.

Figs. 7–8

2002 *Kalotermes ?swinhoei*. – GRIMALDI et al., p. 33, 35, fig. 22f.

Holotype: Imago (Fig. 7), AMNH Bu-313.
Age: Early Cretaceous, latest Albian.
Locus typicus: Myanmar, Kachin, Tanai Village (on Ledo road, 105 km NW Myitkyna).
Etymology: The specific epithet is the Latin term avernalis and means "of Avernus" (Avernus was the term for the nether world and the name, therefore, means "of the nether world").

Diagnosis. – As for the genus (vide supra).

Description. – Imago. Length of head to labral apex 1.30 mm; length of head to mandibular base 0.94 mm; head width 0.89 mm; compound eye diameter 0.20 mm; pronotal length 0.66 mm; pronotal width 0.92 mm; metatibial length 0.89 mm; length of forewing from basal suture to apex 5.0 mm; length of forewing scale 0.89 mm; forewing width 1.58 mm. Integument of head dark brown, remainder brown; microsculpturing not evident. Setae of head and pronotum not evident; wing scale with a few, erect, apically-directed setae basal to claval suture (CuP), additional, shorter, erect to suberect setae beyond claval suture and closer to basal suture (Fig. 8e). Forewing (based on right forewing venation: Fig. 8d) with Rs terminating before wing apex; M terminating at wing apex, with five main branches, first and second with secondary branches, basalmost branch terminating at apical quarter of wing along posterior wing margin; CuA with four main branches, all originating outside wing scale, third with secondary branches shortly after origin, cubital field occupying about two-thirds posterior wing margin. Abdomen incomplete.

Genus *Tanytermes* n. gen.

Type species: *Tanytermes anawrahtai* n. gen. n. sp.

Etymology: The new genus-group name is a combination of the Greek prefix tany (meaning, "long") and *Termes*, the oldest generic name in Isoptera. The name is a reference to the elongate shape, particularly of the head, in this fossil. The name is masculine.

Diagnosis. – Imago. Head elongate (Figs. 9, 10a), posteriormost section tapering slightly to form "neck-like" attachment to prothorax, lateral borders roughly parallel-sided; right mandible (as seen through cleared labrum) with at least two, sharply-pointed marginal teeth, subsidiary tooth not present, apical tooth elongate (Fig. 10a); antenna with 14 articles, flagellar articles progressively larger from base to about midpoint and then approximately equal in length and width until apicalmost article which is slightly more elongate and narrow; compound eyes without anterior emargination, circular, relatively small (Fig. 10a), posteriad of antennal articulation by distance slightly less than compound eye length, separated from lower margin of head by less than eye diameter, separated from posterior border of head by many times eye diameter; ocelli absent; fontanelle absent. Pronotum elongate, longer than wide (Fig. 10a), maximal width slightly less than width of head, relatively flat; anterior border straight; lateral borders slightly convergent anteriorly; posterior border straight. All tarsi tetramerous (Figs. 10c–e); tibial spur formula 2-3-2 (Figs. 10c–e), spurs of all legs minutely serrated; pretarsus with ungues simple, with large arolium present on all legs (Figs. 10c–e). Wing membranes hyaline and not reticulate; veins Sc, R, and Rs heavily pigmented, remainder lightly pigmented; forewing scale large, overlapping hind wing scale, humeral margin almost straight, basal suture convex (Fig. 10a); all veins originating inside wing scale, termination of CuP (claval fissure) on posterior margin well prior to basal cleavage suture (Fig. 10a); Sc terminating on costal margin in basal quarter of wing length, at distance from basal suture slightly less than forewing scale length (Fig. 10b); R simple, terminating at about one-third wing length; Rs first branching in basal third of wing, no inferior branches present, with eight superior branches, the first minutely branched right along anterior wing margin; Rs running generally parallel to costal wing margin for entire length, thereby forming narrow radial field, Rs separate from M along its entire length; M relatively simple, running about half way between Rs and CuA, first branching in apical

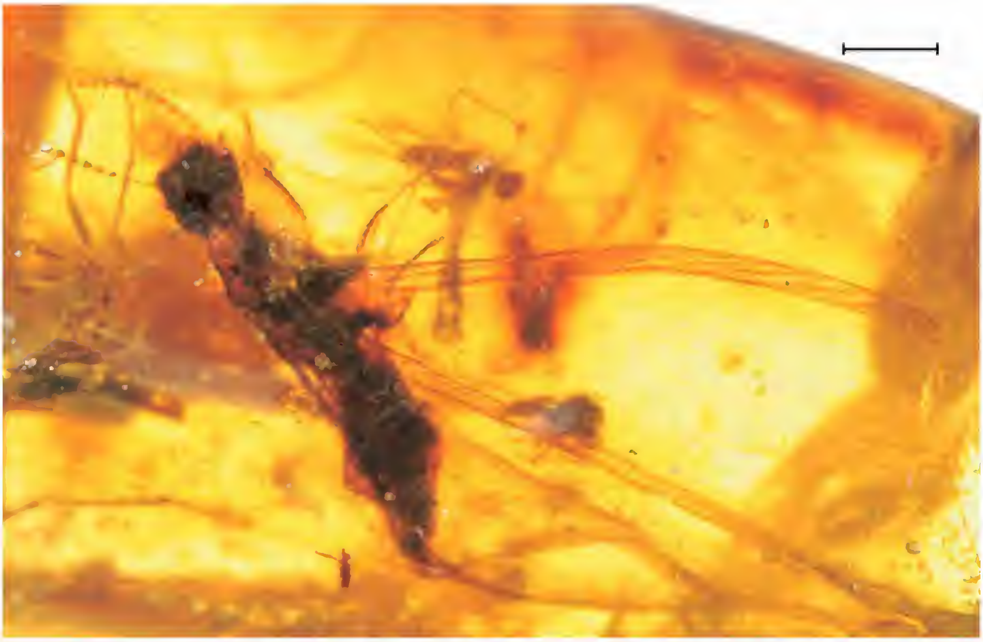

Fig. 9. Photomicrograph of holotype in *Tanytermes anawrahtai* n. gen. n. sp. (AMNH Bu-1608); Burmese amber, latest Albian; Tanai Village, Myanmar. – Scale bar = 1 mm.

third of wing, with first branch terminating at wing apex, forming relatively narrow medial field encompassing wing apex; CuA highly pectinate along its entire length (Fig. 10b), some branches with shorter, apical branches as well, CuA-field encompassing nearly entire posterior margin of forewing. Abdomen relatively narrow, cylindrical; tenth tergum with deep medioapical division (Fig. 10f); cerci not preserved.

Comments. – While the venation of *Tanytermes* n. gen. is generally termopsine-like, other aspects of its morphology are quite autapomorphic. In particular, the elongate, snakefly-like shape of the head, with the exophthalmic compound eyes positioned far anterior on the head is dramatically distinctive and differs from all other Cretaceous Isoptera. In addition, the pronotum is elongate, although still narrower than the head capsule. The venation of *Tanytermes* n. gen. is reminiscent of *Stolotermes* and particularly *Porotermes* owing to the relatively narrow radial field that does not widen near the wing apex, the lack of a connection between Rs and M, with a more simplistic M extending to the wing apex. However, *Tanytermes* n. gen. lacks a subsidiary tooth on the right mandible, has a peculiarly elongate apical tooth, has an elongate pronotum and head capsule, wing membrane that is not reticulate (reticulate in *Porotermes*), a long and extensively branched CuA (much shorter in *Stolotermes* and *Porotermes*, with a corresponding expansion in the branching of M), and it possesses a distinct arolium.

It is worth noting that the “snakefly-like” head and labral shape of *Tanytermes* n. gen. (Figs. 9, 10) is remarkably similar to the overall head structure of soldiers in *Stolotermes* and *Porotermes*, although in both of these the compound eyes are dra-

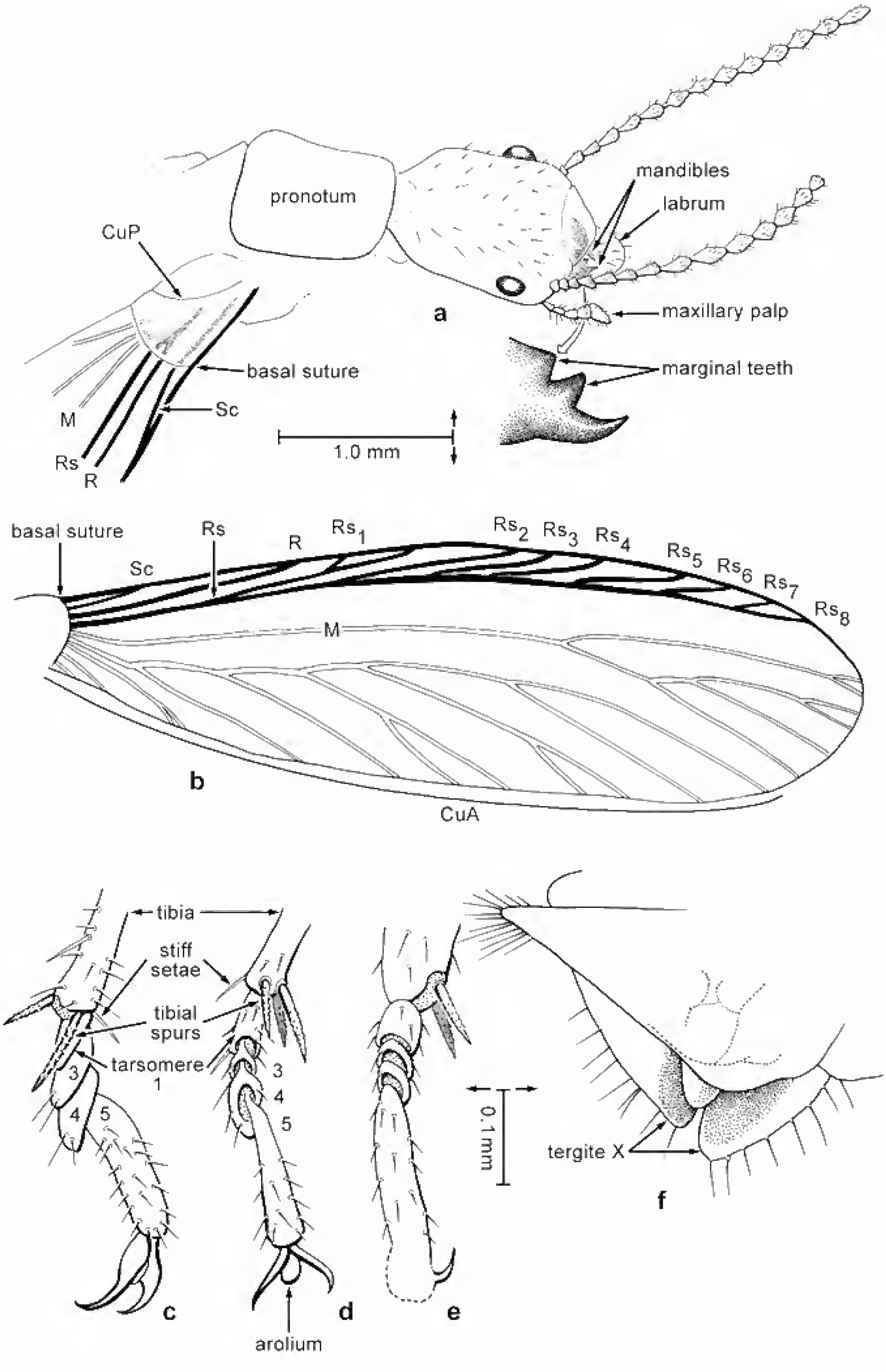
mandibles
labrum
pronotum
CuP
maxillary palp
a
marginal teeth
basal suture
Sc
M
Rs
R
1.0 mm
basal suture
Rs
R
Rs_1
Rs_2
Rs_3
Rs_4
Rs_5
Rs_6
Rs_7
Rs_8
Sc
M
b
CuA
tibia
stiff setae
tibial spurs
tarsomere 1
3
4
5
3
4
5
0.1 mm
tergite X
f
c
d
e
arolium

Fig. 10. Holotype imago of *Tanytermes anawrahtai* n. gen. n. sp. (AMNH Bu-1608); Burmese amber, latest Albian; Tanai Village, Myanmar. **a**: Detail of head, prothorax, and forewing base. **b**: Forewing venation. **c**: Protarsus, propretarsus, and apex of protibia (tarsal articles are numbered based on their homologies with other Isoptera whereby the second tarsal article is reduced and eventually lost, thus leaving only four total articles, but those being present are the first, third, fourth, and fifth, as accordingly numbered in the figure). **d**: Mesotarsus, mesopretarsus, and apex of mesotibia. **e**: Metatarsus, metapretarsus, and apex of metatibia. **f**: Abdominal apex as preserved.

matically reduced and the mandibles are much more elongate and pronounced. Nonetheless, if the head were found in isolation one might suspect it was closer to that of a soldier, than to an imago.

Tanytermes anawrahtai n. gen. n. sp.

Figs. 9–10

Holotype: Imago (Fig. 9), AMNH Bu-1608.
Age: Early Cretaceous, latest Albian.
Locus typicus: Myanmar, Kachin, Tanai Village (on Ledo road, 105 km NW Myitkyna).
Etymology: The specific epithet is a patronymic honoring King ANAWRAHTA who reigned from 1044 A. D. until his death in 1077, and the first ruler of a unified Burmese Empire who also converted the country to Theravada Buddhism.

Diagnosis. – As for the genus (vide supra).

Description. – Imago. Length of head to apex of labrum 1.02 mm; length of head to mandibular base 0.77 mm; head width 0.66 mm; compound eye diameter 0.10 mm; distance from compound eye to lower head margin 0.05 mm; pronotal length 0.66 mm; pronotal width 0.46 mm; metatibial length 0.74 mm; length of forewing with scale 4.95 mm; length of forewing scale 0.51 mm; forewing width 1.53 mm. Integument dark brown except legs brown, microsculpturing of head apparently imbricate, microsculpturing on remainder of body not evident. Head with scattered, short, simple, suberect, anteriorly-directed setae, similar setae on labrum; setae not evident on pronotum. Rs with eight branches, first with short secondary branches at wing margin, Rs terminating just before wing apex; M with four main branches, first and second with short secondary branches at wing margin, M terminating at wing apex, basalmost branch terminating just before wing apex along posterior wing margin; CuA pectinately branched, with nine branches, three originating in wing scale, third, sixth, and seventh branches with short secondary branches, cubital field occupying nearly entire posterior wing margin.

Genus *Proelectrotermes* ROSEN

1913 *Calotermes (Proelectrotermes).* – ROSEN, p. 331. Type species: *Termes (Kalotermes) berendtii* PICTET-BARABAN in: PICTET-BARABAN & HAGEN, 1856, by monotypy.
1941 *Calotermes (Neotermites).* – ARMBRUSTER, p. 18. Type species: *Calotermes (Neotermites) roseni* ARMBRUSTER, 1941, by original designation.

Comments. – The genus *Proelectrotermes* was originally established by ROSEN (1913) as an extinct subgenus of *Kalotermes*, at that time encompassing all kalotermitids. The group was later elevated to generic rank by EMERSON (1942) and combined with *Neotermites* by EMERSON (1971). Since that time the genus has been employed for the middle Eocene, Baltic amber species *P. berendtii* as well as two Tertiary compressions, *P. fodinae* (SCUDDER) from the Eocene-Oligocene boundary of Florissant, Colorado and *P. roseni* (ARMBRUSTER) from the Miocene Randeck Maar near Stuttgart, Germany. Herein we expand the genus to include two other amber fossil species, and extend its range back an additional 50 Ma. KRISHNA (1961) and EMERSON (1969) have provided the most recent, detailed diagnoses for *Proelec-*

trotermes, recognizing the genus as primitive kalotermitids with at least three tibial spurs, with two outer spines and a single inner spine (all seen in the new fossil species described herein). In the forewing of *Proelectrotermes* the radial vein is simple and elongate, extending near to the wing's midlength (or even slightly beyond, as in *P. berendtii*). The kalotermitid fossils considered herein exhibit these same attributes and in the absence of any other distinguishing traits are, accordingly, considered as members of this lineage.

Proelectrotermes swinhoei (Cockerell) n. comb.

1916 *Termopsis swinhoei* n. sp. – Cockerell, p. 138, fig. 4.
1920 *Termopsis swinhoei* Cockerell. – Fletcher, p. 988, pl. 166, fig. 23.
1925 *Termopsis? Swinhoei.* – Snyder, p. 157, chart 1.
1933 *Termopsis swinhoei* Cockerell. – Emerson, p. 190.
1941 *Miotermes? swinhoei* Cockerell. – Armbruster, p. 41.
1949 *Termopsis? swinhoei* Cockerell, 1916. – Snyder, p. 370.
1953 *Termopsis swinhoei* Cockerell. – Lal & Menon, p. 7.
1968 *Kalotermes swinhoei* (Cockerell). – Williams, p. 547, figs. 1–3.
1969 *Kalotermes swinhoei* (Cockerell). – Emerson, p. 34.
1978 *Kalotermes swinhoei* (Cockerell). – Burnham, p. 89.
1978 *Kalotermes swinhoei* (Cockerell, 1916). – Schlüter, p. 55.
1978 *Kalotermes swinhoei* Cock. – Zherikhin, p. 114.
1982 *Kalotermes swinhoe* [sic] (Cockerell, 1916). – Keilbach, p. 214.
1992 *Kalotermes swinhoei* (Cockerell, 1916). – Spahr, p. 30, 79.
1992 *Kalotermes swinhoei* (Cockerell). – Poinar, p. 104.
1993 *Kalotermes swinhœi* (Cockerell, 1916). – Nel & Paicheler, p. 120.
2000 *Kalotermes swinhoei* (Cockerell, 1916). – Ross & York, p. 11, 17, fig. 3.
2002 *Kalotermes swinhoei* (Cockerell). – Grimaldi et al., p. 35.
2005 "*Kalotermes*" *swinhoei.* – Grimaldi & Engel, p. 247.

Holotype: Imago, NHML In. 19096.
Age: Early Cretaceous, latest Albian.
Locus typicus: Northern Myanmar.

Diagnosis. – This species was rather extensively described by Williams (1968) and we have not repeated that material here. Instead we provide only the most salient features for distinguishing the species from other *Proelectrotermes* and for documenting its place in the genus. The venation of this species is very similar to that of *P. holmgreni* n. sp. described below except that M branches apical to the final primary branching of CuA, while in *P. holmgreni* n. sp. the situation is reversed with M first forking well prior to the terminal branching of CuA. The species is also slightly smaller with a forewing length from the basal cleavage suture of 4.81 mm, and forewing width of 1.49 mm (nearly a third of the size of *P. berendtii* in Baltic amber!). Like the Tertiary species of *Proelectrotermes* the metabasitarsus is not distinctly elongate as is the case in *P. holmgreni* n. sp. The legs are unfortunately not sufficiently preserved to determine with accuracy the condition of the tibial spination.

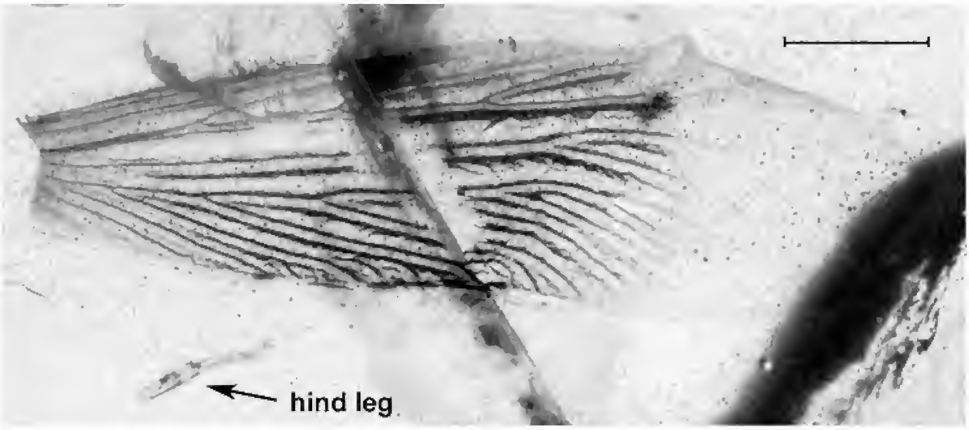

Fig. 11. Photomicrograph of holotype forewing and hind leg fragment (to the lower left of the forewing) of *Proelectrotermes holmgreni* n. gen. n. sp. (AMNH Bu-043); Burmese amber, latest Albian; Tanai Village, Myanmar. – Scale bar = 1 mm.

Proelectrotermes holmgreni n. sp.

Figs. 11–12

Holotype: Fragmentary imago (forewing and hind leg fragment: Fig. 11), AMNH Bu-043.

Age: Early Cretaceous, latest Albian.

Locus typicus: Myanmar, Kachin, Tanai Village (on Ledo road, 105 km NW Myitkyna).

Etymology: The specific epithet is a patronymic honoring of Nils Frithiof Holmgren (1877–1954), the foremost isopterist of his era and perhaps the greatest comparative anatomist of the Isoptera ever. Holmgren developed the first phylogenetic hypotheses for the various groups of termites, recognizing most of the lineages as we understand them today, and laid a sturdy foundation for the subsequent evolutionary studies of Kemner, Emerson, Hare, Krishna, and many others.

Diagnosis. – The new species can be distinguished from all other congeners by the more elongate first tarsomere (apparently of the hind leg) which is slightly longer than the immediately following two tarsal articles (Fig. 12b). In addition, *P. holmgreni* n. sp. is slightly larger than *P. swinhoei* with a forewing length (as measured from the basal cleavage suture) of 6.0 mm and a width of 1.8 mm (refer also to the diagnosis for *P. swinhoei*, vide supra), but about one-half the size of the Baltic amber species, *P. berendtii* (refer to measurements of that species provided by Emerson 1969). In addition, the radial field is slightly broader than in the Tertiary species.

Description. – Imago. Fragmentary specimen represented solely by shed forewing and fragment of hind leg (all other features of the species are unknown). Length of forewing from basal cleavage suture to apex 6.0 mm; width of forewing 1.8 mm; basal suture broadly curved; Sc, R, and Rs more heavily pigmented than M and CuA; Sc and R simple and elongate, Sc terminating on anterior wing margin in basal third of wing (Fig. 12a), R terminating near wing midlength; Rs running parallel to anterior wing margin, with six branches, third branch with minute secondary branches at wing margin, radial field relatively broad, Rs terminating before wing apex; M running at midpoint between Rs and CuA, not branching until apical third

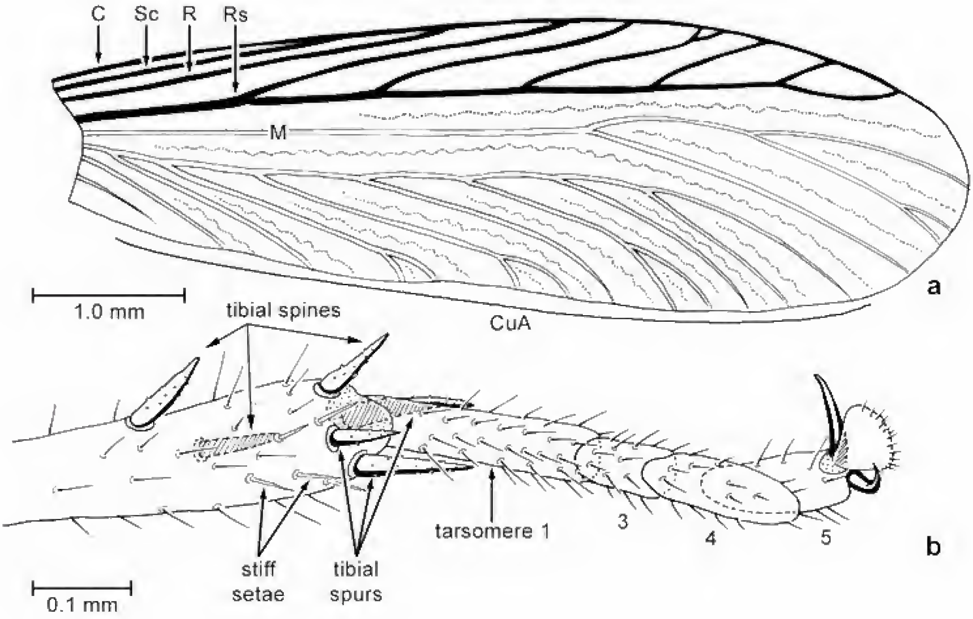

Fig. 12. Holotype of *Proelectrotermes holmgreni* n. sp. (AMNH Bu-043); Burmese amber, latest Albian; Tanai Village, Myanmar. **a**: Forewing venation. **b**: Incomplete hind-leg; metatarsus, metapretarsus, and apex of metatibia (tarsal articles are numbered based on their homologies with other Isoptera whereby the second tarsal article is reduced and eventually lost, thus leaving only four total articles, but those being present are the first, third, fourth, and fifth, as accordingly numbered in the figure).

of wing, with three branches, second branch with minute secondary branches at wing margin, terminal branch of M reaching wing apex, basalmost branch terminating just before wing apex along posterior wing margin; CuA pectinately branched, with ten branches, two originating in wing scale, fourth, fifth, and seventh branches with short secondary branches, cubital field occupying nearly entire posterior wing margin. Three metatibial spurs minutely and sparsely serrate (pimplate); three metatibial spines (one close to arthrodial membrane bearing spurs) (Fig. 12b); metabasitarsus elongate (Fig. 12b), length about equal to combined length of succeeding tarsomeres; arolium present, large; pretarsal ungues simple, not serrate.

Genus *Kachinitermes* n. gen.

Type species: *Hodotermes tristis* Cockerell, 1917.

Etymology: The new genus-group name is a combination of Kachin, the northeastern state of Myanmar from which the amber originates, and *Termes*, the oldest generic name in Isoptera. The name is masculine.

Diagnosis. – Imago. Small, kalotermitid-like species (hind wing length 3.95 mm, as preserved, maximal width 1.17 mm). Wing membrane hyaline, without pigmented nodules; hind wing R terminating on anterior wing margin in basal quarter of wing, shortly beyond basal cleavage suture; Rs with apparently six, simple branches, M basally branching from radial stem in basal quarter of wing, simple along its entire length, running about midway between Rs and CuA; CuA occupying entire posterior margin of wing, with nine main branches, first originating inside wing scale, third, fourth, and fifth branches with secondary branches.

Comments. – The placement of type species has been controversial and, sadly, some of this ambiguity remains. Only a hind wing is preserved, with the extreme apex missing. COCKERELL (1917) originally placed his fossil in *Hodotermes*, without justification, while WILLIAMS (1968) transferred the species to Kalotermitidae and to the genus *Kalotermes* in particular. While it does seem as though attribution to Kalotermitidae is likely accurate, the species does not really appear to have true affinity to *Kalotermes*. Despite the fragmentary nature of the holotype and the degree of deterioration, there is no evidence that the wing membrane ever possessed pigmented nodules as is present in modern *Kalotermes*. Moreover, the hind wing R is much shorter than in modern *Kalotermes*, the vein scarcely extending to one-quarter of the wing length before terminating on the costal margin. The affinity of this new genus among kalotermitids is entirely unknown and we must await the discovery of new, more completely preserved material to elaborate further on its identity with any accuracy.

Kachinitermes tristis (COCKERELL) n. comb.

1917 *Hodotermes tristis* sp. n. – COCKERELL, p. 329, fig. 10.
1920 *Hodotermes tristis* COCKERELL. – FLETCHER, p. 988, pl. 166, fig. 24.
1933 *Hodotermes tristis* COCKERELL. – EMERSON, p. 190.
1941 *Hodotermes tristis* COCKERELL. – ARMBRUSTER, p. 40.
1941 *Rhinotermes? tristis* COCKERELL. – ARMBRUSTER, p. 41.
1949 *Hodotermes tristis* COCKERELL, 1917. – SNYDER, p. 370.
1953 *Hodotermes tristis* COCKERELL. – LAL & MENON, p. 4.
1968 *Kalotermes tristis* (COCKERELL). – WILLIAMS, p. 549, fig. 4.
1969 *Kalotermes tristis* (COCKERELL). – EMERSON, p. 35.
1978 *Kalotermes tristis* (COCKERELL). – BURNHAM, p. 89.
1978 *Kalotermes tristis* (COCKERELL, 1916 [sic]). – SCHLÜTER, p. 55.
1978 *Kalotermes tristis* COCK. – ZHERIKHIN, p. 114.
1982 *Kalotermes tristis* (COCKERELL, 1917). – KEILBACH, p. 214.
1992 *Kalotermes tristis* (COCKERELL, 1917). – SPHAR, p. 30, 79.
1992 *Kalotermes tristis* (COCKERELL). – POINAR, p. 104.
1993 *Kalotermes tristis* (COCKERELL, 1917). – NEL & PAICHELER, p. 120.
2000 *Kalotermes tristis* (COCKERELL, 1917). – ROSS & YORK, p. 11.
2002 *Kalotermes tristis* (COCKERELL). – GRIMALDI et al., p. 35.

Holotype: Imago, NHML In. 19103.
Age: Early Cretaceous, latest Albian.
Locus typicus: Northern Myanmar.

Diagnosis. – As for the genus (vide supra).

Tab. 1. Described Mesozoic Isoptera[1] (presented in order by age, from oldest to most recent). Three additional taxa, not listed or considered further herein since formal descriptions have yet to be published, are reported by Bechly (in press).

Taxon	Locality	Type[2]	Age
Baissatermes lapideus n. gen. n. sp.	Baissa, Transbaikalia, Russia	C	Cretaceous (Berriasian)
Valditermes brenanae Jarzembowski, 1981	Wealden, England	C	Cretaceous (Hauterivian)
Melqartitermes myrrheus n. gen. n. sp.	Lebanese amber	A	Cretaceous (Neocomian)
Meiatermes bertrani Lacasa-Ruiz & Martínez-Delclòs, 1986	Montsec, Spain	C	Cretaceous (Barremian)
Jitermes tsaii Ren, 1995	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
Huaxitermes huangi Ren, 1995	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
Yanjingtermes giganteus Ren, 1995	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
Yongdingia opipara Ren, 1995	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
Asiatermes reticulatus Ren, 1995	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
Mesotermopsis incompleta (Ren, 1995)	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
Mesotermopsis lata (Ren, 1995)	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
Meiatermes araripena Krishna, 1990	Santana, Brazil	C	Cretaceous (Aptian)
Cretatermes pereirai Fontes & Vulcano, 1998	Santana, Brazil	C	Cretaceous (Aptian)
Mariconitermes talicei Fontes & Vulcano, 1998	Santana, Brazil	C	Cretaceous (Aptian)
Caatingatermes megacephalus Martins-Neto et al., 2006[3]	Santana, Brazil	C	Cretaceous (Aptian)
Araripetermes nativa Martins-Neto et al., 2006[3]	Santana, Brazil	C	Cretaceous (Aptian)
Nordestinatermes obesa Martins-Neto et al., 2006[3]	Santana, Brazil	C	Cretaceous (Aptian)
Khanitermes acutipennis (Ponomarenko, 1988), n. comb.	Shar-Tologoy, Mongolia	C	Cretaceous (Aptian)
Kachinitermes tristis (Cockerell, 1917), n. comb.	Burmese amber	A	Cretaceous (Albian)
Proelectrotermes swinhoei (Cockerell, 1916), n. comb.	Burmese amber	A	Cretaceous (Albian)
Proelectrotermes holmgreni n. sp.	Burmese amber	A	Cretaceous (Albian)
Archeorhinotermes rossi Krishna & Grimaldi, 2003	Burmese amber	A	Cretaceous (Albian)
Mylacrotermes cordatus n. gen. n. sp.	Burmese amber	A	Cretaceous (Albian)
Dharmatermes avernalis n. gen. n. sp.	Burmese amber	A	Cretaceous (Albian)
Tanytermes anawrahtai n. gen. n. sp.	Burmese amber	A	Cretaceous (Albian)
Mastotermes sarthensis Schlüter, 1989	French amber	A	Cretaceous (Cenomanian)
Lutetiatermes priscus Schlüter, 1989, nom. emend.	French amber	A	Cretaceous (Cenomanian)
Cretatermes carpenteri Emerson, 1967	Labrador, Canada	C	Cretaceous (Cenomanian)
Carinatermes nascimbenei Krishna & Grimaldi, 2000	New Jersey amber, USA	A	Cretaceous (Turonian)

[1] Although described as a termite, *Hebeitermes weichangensis* Hong (1982) from Jiuquan, Gansu, China (Cretaceous: Barremian) is actually a roach wing.

[2] Type of preservation indicated as amber inclusion (A) or compression fossil (C).

[3] The validity of these taxa is of serious debate and the poor descriptions and figures suggest these may prove to be synonyms, a thorough revision of Cretaceous Isoptera from Brazil is needed from actual isopterists.

4. Discussion

It is interesting to note that the history of Cretaceous termite research, outlined in the introduction, has mimicked that of the discovery and study of Cretaceous ants, another ecologically-ubiquitous and abundant social insect lineage today. As for the termites, the first Cretaceous ant was discovered and described in the late 1960's (WILSON et al. 1967) (note that at the time EMERSON (1967) described the "first" Cretaceous termite COCKERELL's species were mistakenly believed to be of Miocene age), with a few more trickling in during the 1980's (e.g., WILSON 1985; DLUSSKY 1987), but with the real explosion in their study and the full force of their implications not come to fruition until the late 1990's and earliest years of the current century (e.g., DLUSSKY 1996, 1999; GRIMALDI et al. 1997; GRIMALDI & AGOSTI 2000; ENGEL & GRIMALDI 2005). In this way, the studies of these two dominant social animals have mirrored each other. Interestingly, the total number of Cretaceous ants, including the armaniids, is 36 species (again close to the current total for termites) and there too the greatest diversity is from Asiatic deposits (21 species, or an overwhelming 58%, admittedly this may be slightly biased owing to looser species concepts for some of the Asiatic taxa but the fauna remains diverse nonetheless) (ENGEL & GRIMALDI 2005).

The taxa discussed herein demonstrate the great utility Cretaceous fossils will ultimately have in resolving basal relationships within Isoptera. Species such as *Melgartitermes myrrheus* n. gen. n. sp. and *Mylacrotermes cordatus* n. gen. n. sp. exhibit attributes more primitive than any modern termites, particularly in the presence of ventral cervical sclerites and it must be wondered whether some Early Cretaceous species described as compressions may have also exhibited such a trait but is unobservable owing to fidelity of preservation. More importantly, various Cretaceous species have character combinations that will provide unique insights into the resolution of relationships among basal lineages (GRIMALDI, ENGEL & KRISHNA in prep.).

5. References

ANSORGE, J. (1993): Bemerkenswerte Lebensspuren und ?*Cretosphex catalunicus* n. sp. (Insecta; Hymenoptera) aus den unterkretazischen Plattenkalken der Sierra del Montsec (Provinz Lerida, NE-Spanien). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **190**: 19–35.

ARMBRUSTER, L. (1941): Über Insektenstaaten der Vorwelt. 1. Miocäne Randecker Termiten. – Archiv für Bienenkunde, **22**: 3–43.

BECHLY, G. (in press): Isoptera – termites. – In: MARTILL, D. M., BECHLY, G. & LOVERIDGE, R. L. (eds.): The Crato Fossil Beds of Brazil – Window into an Ancient World: 249–262; Cambridge (Cambridge University Press).

BURNHAM, L. (1978): Survey of social insects in the fossil record. – Psyche, **85** (1): 85–133.

COCKERELL, T. D. A. (1916): Insects in Burmese amber. – American Journal of Science, series 4, **42**: 135–138.

COCKERELL, T. D. A. (1917): Insects in Burmese amber. – Annals of the Entomological Society of America, **10** (4): 323–329.

CRUICKSHANK, R. D. & KO, K. (2003): Geology of an amber locality in the Hukawng Valley, northern Myanmar. – Journal of Asian Earth Sciences, **21** (5): 441–455.

DLUSSKY, G. M. (1987): New Formicoidea (Hymenoptera) of the Upper Cretaceous. – Paleontological Journal, **21** (1): 146–150.

DLUSSKY, G. M. (1996): Ants (Hymenoptera, Formicidae) from Burmese amber. – Paleontological Journal, **30** (4): 449–454.

DLUSSKY, G. M. (1999): New ants (Hymenoptera, Formicidae) from Canadian amber. – Paleontological Journal, **33** (4): 409–412.

EMERSON, A. E. (1933): A revision of the genera of fossil and Recent Termopsinae (Isoptera). – University of California Publications in Entomology, **6** (6): 165–196.

EMERSON, A. E. (1942): The relations of a relict South African termite (Isoptera, Hodotermitidae, *Stolotermes*). – American Museum Novitates, **1187**: 1–12.

EMERSON, A. E. (1967): A new genus and species of termite (Isoptera: Hodotermitidae). – Psyche, **74** (4): 276–289.

EMERSON, A. E. (1969): A revision of the Tertiary fossil species of the Kalotermitidae (Isoptera). – American Museum Novitates, **2359**: 1–57.

EMERSON, A. E. (1971): Tertiary fossil species of the Rhinotermitidae (Isoptera), phylogeny of genera, and reciprocal phylogeny of associated Flagellata (Protozoa) and the Staphylinidae (Coleoptera). – Bulletin of the American Museum of Natural History, **146** (3): 243–304.

ENGEL, M. S. & GRIMALDI, D. A. (2005): Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). – American Museum Novitates, **3485**: 1–23.

ENGEL, M. S. & KRISHNA, K. (2004): Family-group names for termites (Isoptera). – American Museum Novitates, **3432**: 1–9.

FLETCHER, T. B. (1920): Indian fossil insects. – Report of the Proceedings of the Third Entomological Meeting [Pusa, 1919], **3**: 983–990.

FONTES, L. R. & VULCANO, M. A. (1998): Cupins fósseis do novo mundo. – In: FONTES, L. R. & BERTI FILHO, E. (eds.): Cupins: O desafio do cohecimento: 243–295; Piracicaba (Fundação de Estudos Agrários Luiz de Queiroz).

GRANDCOLAS, P. (1996): The phylogeny of cockroach families: A cladistic appraisal of morpho-anatomical data. – Canadian Journal of Zoology, **74**: 508–527.

GRANDCOLAS, P. & D'HAESE, C. (2001): The phylogeny of cockroach families: Is the current molecular hypothesis robust? – Cladistics, **17**: 48–55.

GRIMALDI, D. & AGOSTI, D. (2000): A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants. – Proceedings of the National Academy of Sciences, USA, **97** (25): 13678–13683.

GRIMALDI, D. & ENGEL, M. S. (2005): Evolution of the Insects. xv+755 pp.; Cambridge (Cambridge University Press).

GRIMALDI, D., AGOSTI, D. & CARPENTER, J. M. (1997): New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their phylogenetic relationships. – American Museum Novitates, **3208**: 1–43.

GRIMALDI, D. A., ENGEL, M. S. & NASCIMBENE, P. C. (2002): Fossiliferous Cretaceous amber from Myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. – American Museum Novitates, **3361**: 1–72.

HONG, Y.-C. (1982): Mesozoic Fossil Insects of Jiuquan Basin in Gansu Province. 187 pp.; Peking (Geological Publishing House). [In Chinese]

INWARD, D., BECCALONI, G. & EGGLETON, P. (2007): Death of an order: A comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. – Biology Letters, **3** (3): 331–335.

JARZEMBOWSKI, E. A. (1981): An Early Cretaceous termite from southern England (Isoptera: Hodotermitidae). – Systematic Entomology, **6**: 91–96.

JARZEMBOWSKI, E. A. (1991): New insects from the Weald Clay of the Weald. – Proceedings of the Geologist's Association, **102** (2): 93–108.

KEILBACH, R. (1982): Bibliographie und Liste der Arten tierischer Einschlüsse in fossilen Harzen sowie ihrer Aufbewahrungsorte, Teil I. – Deutsche Entomologische Zeitschrift, Neue Folge, **29** (1–3): 129–286.

KLASS, K.-D. & MEIER, R. (2006): A phylogenetic analysis of Dictyoptera (Insecta) based on morphological characters. – Entomologische Abhandlungen, **63** (1–2): 3–50.

KRISHNA, K. (1961): A generic revision and phylogenetic study of the family Kalotermitidae (Isoptera). – Bulletin of the American Museum of Natural History, **122** (4): 303–408.

KRISHNA, K. (1990): Isoptera. – In: GRIMALDI, D. A. (ed.): Insects from the Santana Formation, Lower Cretaceous, of Brazil. – Bulletin of the American Museum of Natural History, **195**: 76–81.

Krishna, K. & Grimaldi, D. (2000): A new subfamily, genus, and species of termite (Isoptera) from New Jersey Cretaceous amber. – In: Grimaldi, D. (ed.): Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey: 133–140; Leiden (Backhuys Publishers).

Krishna, K. & Grimaldi, D. (2003): The first Cretaceous Rhinotermitidae (Isoptera): A new species, genus, and subfamily in Burmese amber. – American Museum Novitates, **3390**: 1–10.

Lacasa-Ruiz, A. & Martínez-Delclòs, X. (1986): *Meiatermes*: Nuevo género fósil de insecto isóptero (Hodotermitidae) de las calizas necomienses del Montsec (Provincia de Lérida, España). 65 pp.; Lleida (Institut d'Estudis Ilerdencs).

Lal, R. & Menon, R. D. (1953): Catalogue of Indian Insects: Part 27 – Isoptera. [4]+94 pp.; Delhi (Government of India Press).

Lo, N., Tokuda, G., Watanabe, H., Rose, H., Slaytor, M., Maekawa, K., Bandi, C. & Noda, H. (2000): Evidence from multiple gene sequences indicates that termites evolved from wood-feeding cockroaches. – Current Biology, **10**: 801–804.

Lo, N., Engel, M. S., Cameron, S., Nalepa, C. A., Tokuda, G., Grimaldi, D., Kitade, O., Krishna, K., Klass, K.-D., Maekawa, K., Miura, T. & Thompson, G. J. (2007): Save Isoptera: A comment on Inward et al. – Biology Letters, **3** (5): 562–563.

Martín-Closas, C. & López-Morón, N. (1995): The Charophyte flora. – In: Martínez-Delclòs, X. (ed.): Montsec and Montral-Alcover. Two Konservat Lagerstätten, Catalonia, Spain. II International Symposium on Lithographic Limestones Field Trip Book: 29–31; Lleida (Institut d'Estudis Ilerdencs).

Martínez-Delclòs, X. & Martinell, J. (1995): The oldest known record of social insects. – Journal of Paleontology, **69** (3): 594–599.

Martins-Neto, R. G., Ribeiro-Júnior, C. & Prezoto, F. (2006): New fossils (Isoptera: Hodotermitidae), from the Santana Formation (Lower Cretaceous, Araripe Basin, Northeast Brazil), with descriptions of new taxa including a new subfamily. – Sociobiology, **47** (1): 125–134.

McKittrick, F. A. (1964): Evolutionary studies of cockroaches. – Memoirs of the Cornell University Agricultural Experiment Station, **389**: 1–197.

Nascimbene, P. & Silverstein, H. (2000): The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. – In: Grimaldi, D. (ed.): Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey: 93–102; Leiden (Backhuys Publishers).

Nel, A. & Paicheler, J.-C. (1993): Les Isoptera fossiles. État actuel des connaissances, implications paléoécologiques et paléoclimatologiques (Insecta, Dictyoptera). – Cahiers de Paléontologie, **1993**: 101–179.

Pictet-Baraban, F.-J. & Hagen, H. A. (1856): Die im Bernstein befindlichen Neuropteren der Vorwelt. – In: Berendt, G. C. (ed.): Die im Bernstein befindlichen organischen Reste der Vorwelt [volume 2]: 41–126; Berlin (Nicolaische Buchhandlung).

Poinar, G. O., Jr. (1992): Life in Amber. xiii+[i]+350 pp.; Stanford (Stanford University Press).

Ponomarenko, A. G. (1988): New Mesozoic insects. – Transactions of the Joint Soviet-Mongolian Paleontological Expedition, **33**: 71–80. [In Russian]

Rasnitsyn, A. P. & Quicke, D. L. J. (eds.) (2002): History of Insects. xii+517 pp.; Dordrecht (Kluwer Academic Publishers).

Rasnitsyn, A. P., Jarzembowski, E. A. & Ross, A. J. (1998): Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and paleoenvironmental significance. – Cretaceous Research, **19** (3–4): 329–391.

Ren, D. (1995): Isoptera Comstock, 1895. – In: Ren, D., Lu, L., Guo, Z. & Ji, S. (eds.): Faunae and Stratigraphy of Jurassic-Cretaceous in Beijing and the Adjacent Areas: 56–61; Beijing (Seismic Publishing House). [In Chinese, with English summary]

Roonwal, M. L. & Sen-Sarma, P. K. (1960): Contributions to the systematics of oriental termites. xiv+275 pp.; New Delhi (Indian Council of Agricultural Research – Entomological Monographs 1).

ROSEN, K. VON (1913): Die fossilen Termiten: Eine kurze Zusammenfassung der bis jetzt bekannten Funde. – In: JORDAN, K. & ELTRINGHAM, H. (eds.): Transactions of the 2nd International Congress of Entomology [volume II]: 318–335; London (Hazell, Watson, and Viney).

ROSS, A. J. & YORK, P. V. (2000): A list of type and figured specimens of insects and other inclusions in Burmese amber. – Bulletin of the Natural History Museum (London), Geology Series, **56** (1): 11–20.

SCHLÜTER, T. (1978): Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. – Berliner geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie, **9**: 1–150.

SCHLÜTER, T. (1989): Neue Daten über harzkonservierte Arthropoden aus dem Cenomanium NW-Frankreichs. – Documenta Naturae, **56** (5): 59–70.

SNYDER, T. E. (1925): Notes on fossil termites with particular reference to Florissant, Colorado. – Proceedings of the Biological Society of Washington, **38**: 149–166.

SNYDER, T. E. (1949): Catalog of the termites (Isoptera) of the world. – Smithsonian Miscellaneous Collections, **112**: 1–490.

SPAHR, U. (1992): Ergänzungen und Berichtigungen zu R. KEILBACHS Bibliographie und Liste der Bernsteinfossilien – Klasse Insecta [Ausgenommen: "Apterygota", Hemipteroidea, Coleoptera, Hymenoptera, Mecopteroidea]. – Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie), **182**: 1–102.

THORNE, B. L., GRIMALDI, D. A. & KRISHNA, K. (2000): Early fossil history of termites. – In: ABE, T., BIGNELL, D. E. & HIGASHI, M. (eds.): Termites: Evolution, Sociality, Symbioses, Ecology: 77–93; Dordrecht (Kluwer Academic Publishers).

WILLIAMS, R. M. C. (1968): Redescriptions of two termites from Burmese amber. – Journal of Natural History, **2**: 547–551.

WILSON, E. O. (1985): Ants from the Cretaceous and Eocene amber of North America. – Psyche, **92**: 205–216.

WILSON, E. O., CARPENTER, F. M. & BROWN, W. L., JR. (1967): The first Mesozoic ants, with the description of a new subfamily. – Psyche, **74**: 1–19.

ZHERIKHIN, V. V. (1978): Development and changes of the Cretaceous and Cenozoic faunal assemblages (Tracheata and Chelicerata). – Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR, **165**: 1–198. [In Russian]

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A synopsis of Baltic amber termites (Isoptera)

MICHAEL S. ENGEL, DAVID A. GRIMALDI & KUMAR KRISHNA

Abstract

A brief overview and dichotomous key is provided for those termites (Isoptera) occurring in middle Eocene (Lutetian) Baltic amber. Ten species in seven genera are presently documented from Baltic amber, these being as follows: *Garmitermes succineus* n. gen. n. sp., *Termopsis bremii* (HEER), *T. ukapirmasi* n. sp., *Archotermopsis tornquisti* ROSEN, *Proelectrotermes berendtii* (PICTET-BARABAN), *Electrotermes affinis* (HAGEN), *E. girardi* (GIEBEL), *Reticulitermes antiquus* (GERMAR), *R. minimus* SNYDER, and *Parastylotermes robustus* (ROSEN). *Garmitermes succineus* n. gen. n. sp. is the first *Mastotermes*-like termite discovered in Baltic amber. *Hemerobites* GERMAR, a senior synonym of *Reticulitermes* HOLMGREN, is designated as a nomen oblitum under the ICZN rules. *Maresa* GIEBEL, another senior synonym of *Reticulitermes*, is tentatively suppressed pending a petition to the ICZN to preserve the latter name.

Keywords: Amber, distribution, Isoptera, paleontology, taxonomy, termite, Tertiary, Eocene.

Zusammenfassung

Es wird ein kurzer Überblick über die Termiten (Isoptera) aus dem Mitteleozän des Baltischen Bernsteins gegeben sowie ein dichotomer Bestimmungsschlüssel für diese Arten erstellt. Die folgenden sieben Gattungen mit zehn Arten sind gegenwärtig aus dem Baltischen Bernstein dokumentiert: *Garmitermes succineus* n. gen. n. sp., *Termopsis bremii* (HEER), *T. ukapirmasi* n. sp., *Archotermopsis tornquisti* ROSEN, *Proelectrotermes berendtii* (PICTET-BARABAN), *Electrotermes affinis* (HAGEN), *E. girardi* (GIEBEL), *Reticulitermes antiquus* (GERMAR), *R. minimus* SNYDER und *Parastylotermes robustus* (ROSEN). *Garmitermes succineus* n. gen. n. sp. ist die erste *Mastotermes*-ähnliche Termite, die im Baltischen Bernstein entdeckt worden ist. *Hemerobites* GERMAR, ein älteres Synonym von *Reticulitermes* HOLMGREN, wird entsprechend den Regeln der ICZN als nomen oblitum eingestuft. *Maresa* GIEBEL, ein weiteres älteres Synonym von *Reticulitermes*, wird vorläufig unterdrückt, bis über den Antrag an die ICZN, den letzteren Namen beizubehalten, entschieden ist.

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1. Introduction

Baltic amber has an ancient allure. PLINY the Elder (GAIUS PLINIUS SECUNDUS, 23–79 A. D.) recorded that during the reign of NERO CLAUDIUS CAESAR AUGUSTUS GERMANICUS (37–68 A. D., reigned 54–68 A. D., last of the Julio-Claudian Dynasty) the value of an amber object exceeded that of a healthy, male slave, so great was the emperor's passion for the prized commodity. At the same time, many gazed with awe at the insects elegantly preserved therein and even the great Roman poet MARCUS VALERIUS MARTIALIS (c. 40–c. 103 A. D.) composed epigrams immortalizing the insects he observed in succinite. The same intrigue with Baltic amber inclusions continues today, although with a more refined view that they represent species from the long extinct tropical forests of the Eocene epoch. The Eocene was the last global "hot house" climate, and Europe was covered by seasonal paratropical forests, with the southern portions of the continent composed of archipelagos in a warm, relatively shallow sea. It was during this Early Paleogene episode (i. e., Paleocene-Eocene) when termites (order Isoptera) appear to have risen to dominance (GRIMALDI & ENGEL 2005). The Tertiary termite fauna is, therefore, of considerable significance for understanding the formation of modern termite diversity.

Herein we provide a brief overview of the Baltic amber termite fauna. Most species have received relatively recent and thorough treatments by other authors and so we provide only a brief review of those genera occurring in Baltic amber and provide descriptions for two new species (one in a new genus). The rhinotermitids have been thoroughly described by EMERSON (1971), the kalotermitids by KRISHNA (1961) and EMERSON (1969), and the termopsines by EMERSON (1933). In addition, WEIDNER (1955) provided a brief account of each species known to him and these were subsequently catalogued by KEILBACH (1982) and SPAHR (1992).

The age and origin of Baltic amber has been discussed by various authors, most recently by ENGEL (2001), WEITSCHAT & WICHARD (2002), and GRIMALDI & ENGEL (2005). The types of the new species are deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, American Museum of Natural History, New York (AMNH).

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2. Systematic paleontology

2.1. Key to termites in Baltic amber

The following key is based solely on imagoes, the only caste hitherto known from Baltic amber.

1 Metatarsus pentamerous, either completely or cryptically (i. e., with second tarsomere not evident in dorsal aspect, but visible in lateral or ventral aspect) 2
– Metatarsus tetramerous or trimerous 5
2 Ocelli absent; pronotum narrower than head; costal area of forewing scale relatively narrow; cleavage suture of forewing weakly arched; hind wings with defined cleavage suture 3
– Ocelli present; pronotum much broader than head, saddle-shaped; costal area of forewing scale large; cleavage suture of forewing strongly arched; hind wings without cleavage suture, torn when shed .... ***Garmitermes succineus*** n. gen. n. sp.
3 Compound eye circular, not enlarged, anterior border not concave or emarginate; metatarsus completely pentamerous; antenna with 22–24 articles 4
– Compound eye large, anterior border distinctly concave; metatarsus cryptically pentamerous (i. e., with second tarsal article visible ventrally but hidden dorsally); antenna with 18–19 articles .... ***Archotermopsis tornquisti*** Rosen
4 Length of forewing from basal cleavage suture ca. 14.8–16.2 mm; forewing basal suture complete, clearly meeting posterior margin; stems of Rs and M joined for short distance in forewing scale .... ***Termopsis bremii*** (Heer)
– Length of forewing from basal cleavage suture ca. 12 mm; forewing basal suture evanescent in posterior third; stems of Rs and M separate in forewing scale .... ***Termopsis ukapirmasi*** n. sp.
5 Fontanelle absent; tarsi tetramerous; wing membrane wrinkled or with weak reticulations between some of the longitudinal veins 6
– Fontanelle present; tarsi trimerous or tetramerous; wing membrane densely reticulate between veins (Fig. 10b) 8
6 Mesotibia with two outer spines, inner spine absent; R terminating on anterior wing margin in basal third of forewing; CuP (claval fissure) terminating on posterior margin prior to basal suture; 15–18 antennal articles 7
– Mesotibia with two outer spines and one inner spine; R terminating on anterior wing margin near forewing midpoint; CuP (claval fissure) terminating at posterior edge of basal suture; 19–20 antennal articles .... ***Proelectrotermes berendtii*** (Pictet-Baraban)
7 Forewing length with scale 8.84–8.94 mm .... ***Electrotermes affinis*** (Hagen)
– Forewing length with scale 6 mm .... ***Electrotermes girardi*** (Giebel)
8 Setae of head and pronotum sparse and short (setae distinctly shorter than length of scape); pronotum slightly narrower than head; tarsi tetramerous 9
– Setae of head and pronotum more numerous and long, particularly on the latter (setae as long as or longer than scape); pronotum distinctly narrower than head; tarsi trimerous .. .. ***Parastylotermes robustus*** (Rosen)
9 Body size moderate, length of forewing from suture 6.5–8.8 mm; antenna with 17–20 articles; ocellus separated from compound eye by slightly less than ocellar width; anterior border of pronotum with slight medial indentation ..... ***Reticulitermes antiquus*** (Germar)
– Body size minute, length of forewing from suture 3.94 mm; antenna with 13–14 articles; ocellus separated from compound eye by ocellar width; anterior border of pronotum straight .... ***Reticulitermes minimus*** Snyder

2.2. Baltic amber genera and new species

The following account provides brief comments on those termite genera occurring in Baltic amber. In addition, we include the description of the two new species (one in a new genus) and discuss the status of the previously proposed taxa. Family-group names follow those of Engel & Krishna (2004a, 2004b, 2007).

Family Mastotermitidae Desneux, 1904a

Genus *Garmitermes* n. gen.

Type species: *Garmitermes succineus* n. sp.

Etymology: The new genus-group name is a combination of the names Garm, from Norse mythology, and *Termes*, meaning termite and the type genus of Isoptera. Garm was the Cerberus of Norse mythology, and was a giant, ferocious dog living in the cave Gnipahellir and guarding Helheim, land of the dead (ruled by Hel, goddess of the underworld). The name is masculine.

Diagnosis. – Head robust and approximately circular, lateral borders parallel-sided (Figs. 1–2a), distinctly opisthognathous; Y-shaped coronal (epicranial) ecdysial cleavage line very faint (Fig. 2a); compound eyes large, circular; ocelli present, large, adjoining compound eyes (Fig. 2a); fontanelle absent; antenna moniliform, with 26 articles, distinctly tapered for apical 7–8 articles; occipital carina present (Fig. 3). Lateral cervical sclerites enlarged (Fig. 3). Pronotum very large, saddle-shaped (covering most of prothoracic pleura) (Figs. 1–2a), anterior margin weakly concave, lateral margins gently converging posteriorly, medio-posterior margin almost straight. Metascutellum broad, plate-like, slightly projecting posteriorly over abdominal base. Procoxae with distinct ventral carina (i. e., "procoxae keeled"); tibial spur formula 3-5-4, spurs stout, asymmetrical, each with ventral concavity, minutely serrate (Fig. 2b, c); protibia without subapical spines; mesotibia with two outer spines; metatibia with a single, subapical spine; all tarsi completely pentamerous, with distinct plantular pads (Fig. 2b, c), with papillae, present on apico-ventral surfaces of basal four tarsal articles; pretarsal ungues simple, arolium either greatly vestigial or absent (a small stub can be seen between the ungues that is either the apex of the unguitractor or perhaps a highly reduced arolium). Forewing scale large, almost entirely covering hind wing base (Figs. 1–2a), heavily sclerotized and pigmented (nearly tegminous), apical margin broadly convex, humeral margin broadly convex, intersects CuP, with broad costal area (as in *Mastotermes*); fine fracture between R and M (as in *Mastotermes*) (Fig. 2a); claval area with scattered, faint dimples (rudimentary archedictyon); CuP (claval fissure) broadly arched, terminating at posterior edge of basal suture; venation of scale distinctly corrugated, pattern of venation as in *Mastotermes*, with all veins originating in scale, single stems of Sc and R, Rs pectinately branching in scale (two branches within scale), M+CuA stem giving rise to M and CuA, the latter forming two branches in scale; distinct reticulations present between CuA and CuP (claval fissure). Hind wing without basal suture, margin roughly torn. Sternites narrow, apical sternite with posterior margin cleft along medial line of sternite (cleft extends approximately one-third sternal length); two slightly protruding lobes at apex of sternite (perhaps membranous) (Fig. 3a); cerci extending beyond abdominal apex, segmentation not discernible (perhaps with at least four articles but this is entirely uncertain and total number of articles, if any, is not ascertainable as the cerci are largely obscured), densely covered with stout, apically-directed setae (styli are also likely present but obscured).

Comments. – *Garmitermes* is the first mastotermitid-like fossil discovered in Baltic amber. Like *Mastotermes*, *Garmitermes* has a large pronotum that is broader than the head, ocelli, has a large forewing scale that almost completely overlaps the hind wing base, the hind wings torn rather than shed along a basal suture, a radial fracture, the tarsi of all legs completely pentamerous, and a primitive 3-5-4 tibial

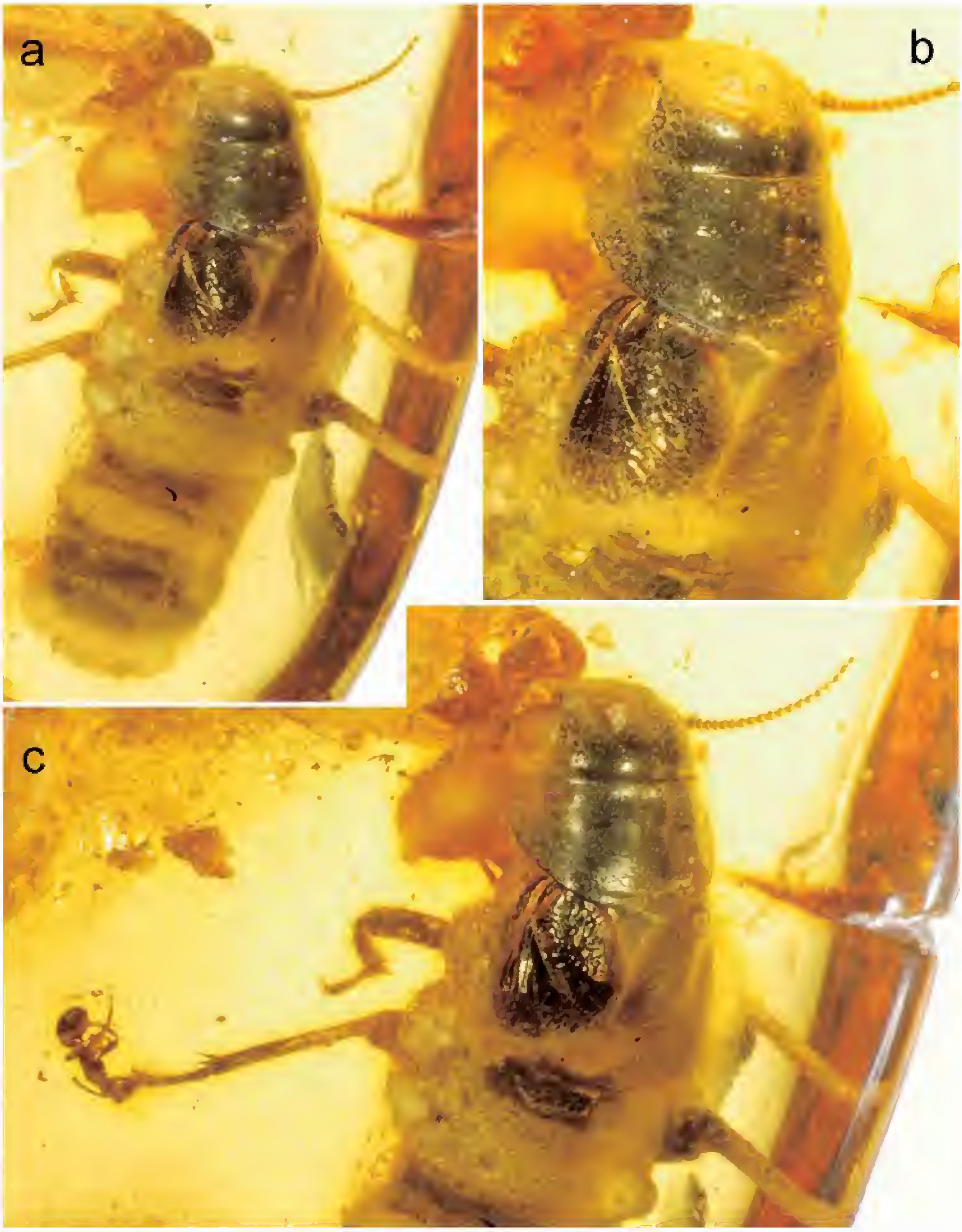

Fig. 1. Dealate imago of *Garmitermes succineus* n. gen. n. sp., holotype (AMNH B-JH-118). **a**: Dorsal aspect. **b**: Detail of head, pronotum, and forewing scales. **c**: Anterior half of specimen showing extended hind leg with worker of *Liometopum oligocenicum* Wheeler grasping tarsus. The pronotum serves as the best scale for all images, the median length being 2.20 mm.

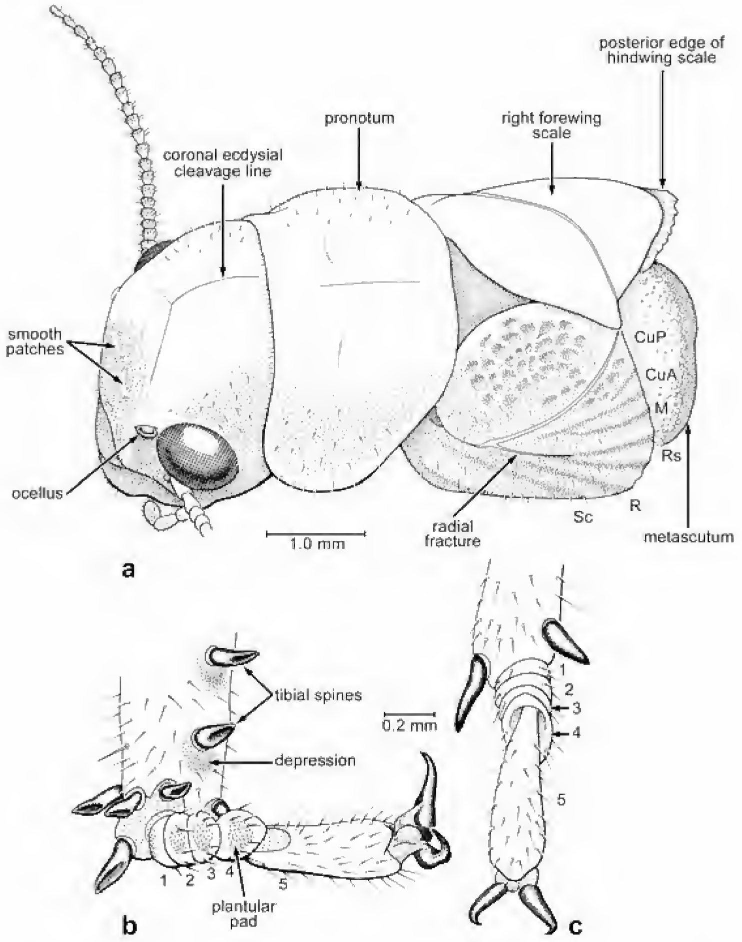
posterior edge of hindwing scale
pronotum
right forewing scale
coronal ecdysial cleavage line
smooth patches
CuP
CuA
M
Rs
ocellus
R
Sc
radial fracture
1.0 mm
metascutum
a
tibial spines
0.2 mm
depression
1
2
3
4
5
plantular pad
b
1
2
3
4
5
c

Fig. 2. *Garmitermes succineus* n. gen. n. sp., holotype (AMNH B-JH-118). **a**: Oblique dorsal view of head and thorax. **b**: Detail of mid leg showing mesotarsus and mesotibial apex as preserved; view of mesotibia is slightly distal looking proximad, view of mesotarsus is ventral. **c**: Detail of foreleg showing protarsus and protibial apex in dorsal view.

spur formula. In contrast to *Mastotermes*, the head is opisthognathous, the lateral cervical sclerites are distinctly larger, the pronotum extremely bowed and wrapped laterally, the metascutellum is greatly enlarged, the mesosternum is well-developed (Fig. 3b), the arolium of the new genus is either greatly vestigial or absent, the tarsal plantular pads are present on the ventro-apical surfaces of the basal four tarsal articles, the number of antennal articles is reduced (26 in *Garmitermes* versus 29–32 in *Mastotermes*) and the apical articles are tapered. We have retained *Garmitermes* in the Mastotermitidae pending the results of an on-going phylogenetic analysis of basal living and fossil termites (Grimaldi, Engel & Krishna in prep.).

Mastotermes is well documented in the Tertiary faunas of Europe, including the roughly contemporaneous fauna of Eckfeld Maar in Germany (Wappler & Engel 2006). Accordingly, it had been considered somewhat enigmatic that mastotermitids were unknown from the Baltic amber fauna. Indeed, Nel & Bourget (2006), not-

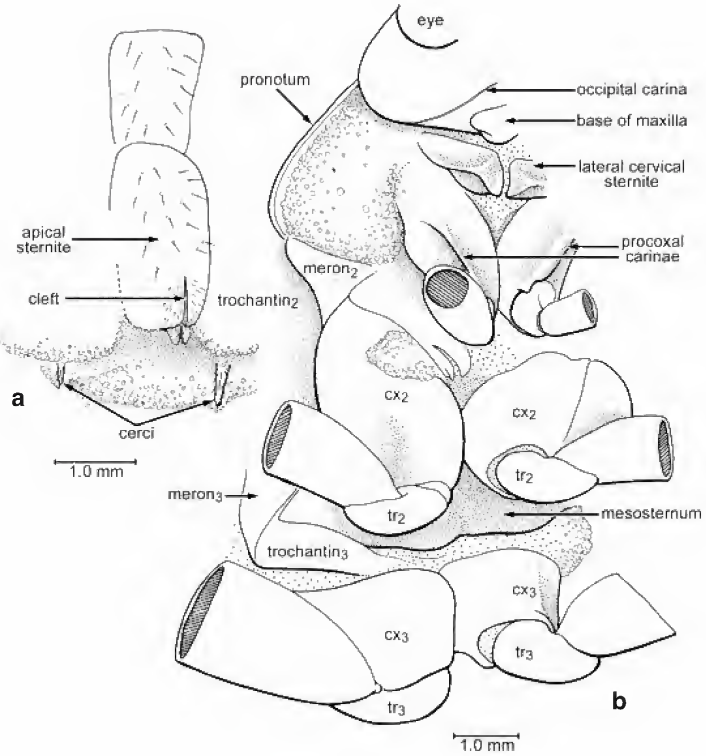
eye
pronotum
occipital carina
base of maxilla
lateral cervical sternite
procoxal carinae
apical sternite
cleft
trochantin2
meron2
a
cerci
1.0 mm
cx2
cx2
tr2
tr2
meron3
mesosternum
trochantin3
cx3
cx3
tr3
tr3
b
1.0 mm

Fig. 3. Ventral structures of *Garmitermes succineus* n. gen. n. sp., holotype (AMNH B-JH-118). **a**: apex of abdomen, showing those structures obscured by froth and bubbles, depicted are the apical two sternites and apices of cerci. **b**: ventral view of thorax and extreme posterior of head.

ing this conspicuous absence, suggested that mastotermitids are preserved only in ambers of angiosperm origin and that the chemical composition of the coniferous resin comprising Baltic amber had a "repulsive action" on such termites. The discovery of the mastotermitid *G. succineus* n. gen. n. sp. in Baltic amber now nicely eliminates that absence and clearly the chemical composition of succinite has not served as an effective repellent.

Garmitermes succineus n. gen. n. sp.

Figs. 1–3

Holotype: Imago (Fig. 1); AMNH B-JH-118; middle Eocene (Lutetian), "Blaue Erde" deposit, Baltic amber.
Etymology: The specific epithet is the Latin term succineus, meaning "amber".

Diagnosis. – As for the genus (vide supra).

Description. – Imago. Length of head to mandibular base 2.70 mm; head width 2.50 mm; compound eye diameter 1.07 mm; distance between compound eye and lower head margin 0.26 mm; ocellar length 0.30 mm; maximum length of pronotum

2.50 mm; median length of pronotum 2.20 mm; width of pronotum 3.80 mm; metatibial length 3.06 mm; length of forewing scale 2.86 mm. Integument faintly imbricate, apparently dark brown on head, pronotum, and wing scales; antennae light brown; legs brown; abdomen (where evident through Schimmel) apparently brown. Head and pronotum with exceedingly sparse pilosity, mostly confined to margins, setae short (length of setae shorter than ocellar length); forewing scale with scattered, erect, short setae, mostly in anterior half.

Comments. – Interestingly, the holotype is preserved with a small worker ant, apparently of *Liometopum oligocenicum* WHEELER (Hymenoptera: Formicidae: Dolichoderinae), biting its apicalmost metatarsomere (Fig. 1c); evidence that the bitter feud between termites and ants has lasted far longer than the battles between the tribes and nations of men.

Family Termopsidae HOLMGREN, 1911

Genus *Termopsis* HEER, 1849

1849 *Termes (Termopsis).* – HEER, p. 23. Type species: *Termes bremii* HEER, 1849, by subsequent designation of ICZN (2005).

1913 *Xestotermopsis.* – ROSEN, p. 329. Type species: *Termes bremii* HEER, 1849, by original designation.

Comments. – The genus *Termopsis* was originally established as a subgenus of *Termes* (at that time encompassing all known termites) but was quickly elevated to generic rank as LINNAEUS's genus was subdivided. Four species are presently classified in *Termopsis*, although only one of these, namely the type species *T. bremii*, is found in Baltic amber. The other three species are known only as later Tertiary compressions: *T. gracilipennis* THÉOBALD from the Oligocene of France, *T. mallaszi* PONGRÁCZ and *T. transsylvanica* PONGRÁCZ from the Miocene of Hungary. Among termopsine termites, *Termopsis* can be immediately recognized by the compound eyes circular, not prominent or large (Figs. 5a, 7a); the absence of ocelli; the pronotum slightly narrower than head, with its lateral borders about parallel to weakly convergent posteriorly; the completely pentamerous tarsi (but see *T. ukapirmasi*, infra), with all five articles visible in dorsal as well as ventral aspect; the absence of the arolium (but see *T. ukapirmasi*, infra); the forewing basal suture only slightly curved (nearly straight); and the long cerci, extending beyond the apex of the abdomen but not elongate as in *Archotermopsis* and with 5–6 articles. Herein we describe a second, much smaller, species of *Termopsis*.

Termopsis ukapirmasi n. sp.

Figs. 4, 5–6

Holotype: Imago (Fig. 4); AMNH B-JH-Iso4; middle Eocene (Lutetian), "Blaue Erde" deposit, Baltic amber.

Paratype: Imago; AMNH B-JH-Iso2; middle Eocene (Lutetian), "Blaue Erde" deposit, Baltic amber.

Etymology: The specific epithet is taken from ancient Prussian mythology and is the name, UKAPIRMAS, of the god who created the world.

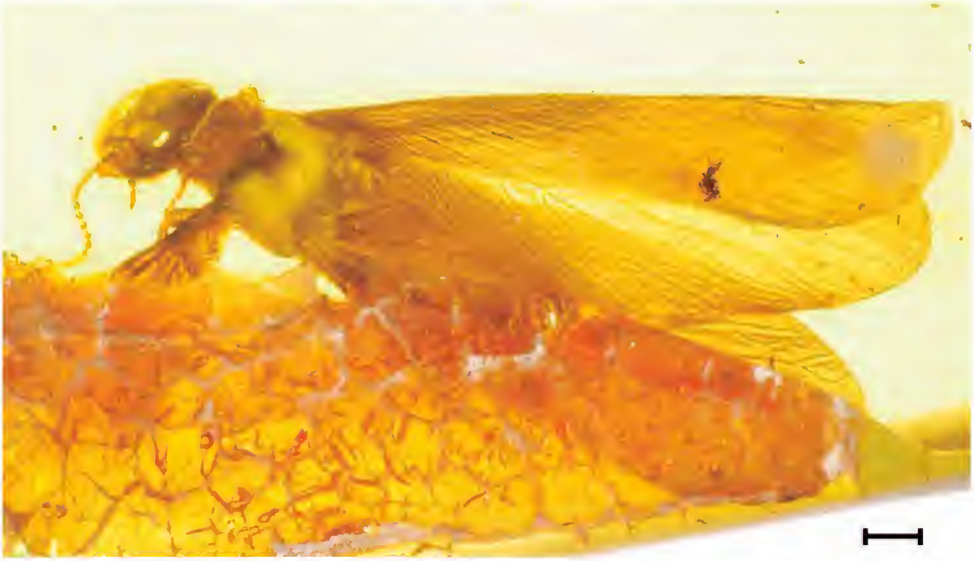

Fig. 4. Imago of *Termopsis ukapirmasi* n. sp., holotype (AMNH B-JH-Iso4). – Scale bar = 1 mm.

Diagnosis. – The new species can be readily distinguished from the only other *Termopsis* in Baltic amber, *T. bremii* (Fig. 7), by the smaller body size, the form and venation of the wing scale, and the posteriorly evanescent basal suture and claval fissure (CuP) (vide etiam Key, supra). In overall size the new species approximates *Archotermopsis tornquisti* from which it can be distinguished by the smaller and circular compound eye, the 23 antennal articles, and the pentamerous tarsi, among other characters distinguishing these two genera.

Description. – Imago. Total length with wings 16.2 mm; body length 10.5 mm; length of head to mandibular base 1.80 mm; head width 2.10 mm; compound eye diameter 0.59 mm; distance between compound eye and lower head margin 0.23 mm; maximum length of pronotum 1.07 mm; width of pronotum 1.99 mm; metatibial length 2.65 mm; forewing length to basal suture 12.0 mm; forewing width 4.1 mm; length of forewing scale 1.33 mm. Integument, where evident, faintly imbricate. Head rounded and dark brown; compound eyes not large, circular, not prominent (Fig. 5a); separated from posterior border of head by nearly twice their diameter; antenna with 23 articles, brown; head with exceedingly sparse, short, erect to suberect setae. Pronotum brown, slightly narrower than head, anterior margin faintly concave, lateral borders weakly converging posteriorly, posterior border almost straight; setae exceedingly short, suberect, and sparse, mostly on lateral borders. Legs brown; tibial spur formula 3-4-3 (Fig. 5c, d); protibia with three apical spurs, without spines; mesotibia with four apical spurs, with one subapical spine; metatibia with three apical spurs, with one subapical spine; arolium present. Forewing scale with all veins originating inside scale; humeral margin with weakly arched lobe present, otherwise relatively straight (Fig. 5a: depicted as preserved with the lobe partially folded ventral to the plane of the wing); forewing basal suture evanescent in posterior third; CuP (claval fissure) evanescent near posterior wing margin, relative-

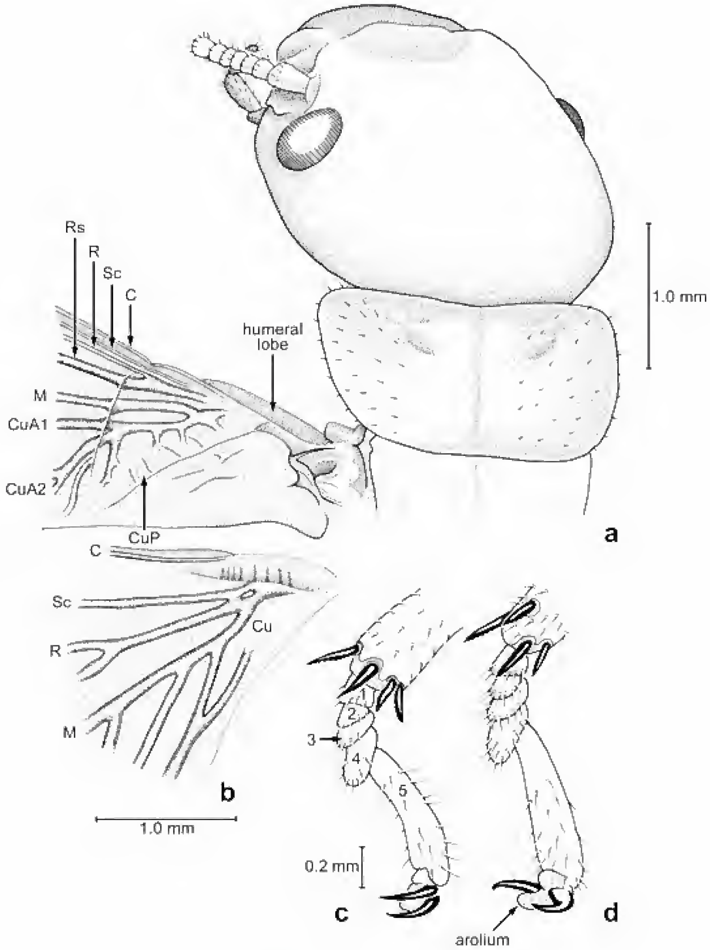

Fig. 5. *Termopsis ukapirmasi* n. sp., holotype (AMNH B-JH-Iso4). **a**: Head, thorax, and base of left forewing. **b**: Base of left hind wing. **c**: Left mesotarsus and mesotibial apex, mesal view. **d**: Right metatarsus and metatibial apex, ventro-mesal view.

ly straight (Fig. 5a); some faint reticulation present between CuA and CuP (claval fissure) and in claval area; veins Sc, R, and Rs (except inferior branches and apicalmost stub) more heavily pigmented than other veins (Fig. 6); Sc short, terminating on anterior wing margin shortly beyond basal suture; R simple and short, terminating on anterior wing margin in basal quarter of wing; radial field gradually widening toward and encompassing wing apex; Rs with six superior branches and three inferior branches, branches without secondary branches, last (apicalmost) four branches not sclerotized; M running closer to CuA than to Rs, attached to CuA in basal third of wing; CuA pectinately branched, with at least seven principal branches; well developed archedictyon (reticulations between main branches) present (Fig. 6); wing hyaline except scale brown, stems of veins M and CuA near basal suture brown (Sc, R, and Rs are uniformly brown as noted), and radial field slightly fuscous; wing membrane wrinkled between veins and archedictyon. Abdomen brown, where evident.

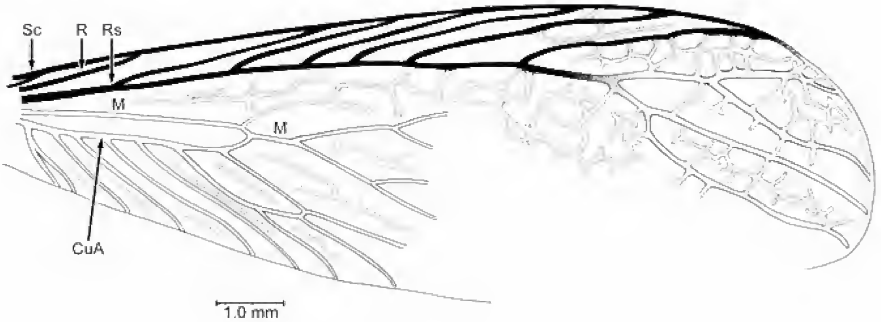
Sc
R
Rs
M
M
CuA
1.0 mm

Fig. 6. Forewing of *Termopsis ukapirmasi* n. sp., holotype (AMNH B-JH-Iso4), omitting basal scale.

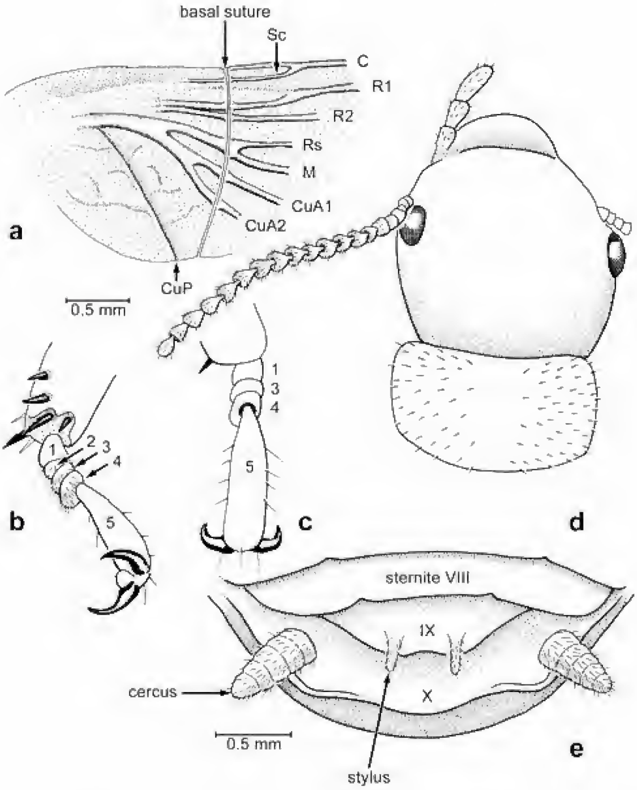
basal suture
Sc
C
R1
R2
Rs
M
CuA1
CuA2
CuP
a
0.5 mm
1
2
3
4
5
b
1
3
4
5
c
d
sternite VIII
IX
X
cercus
stylus
0.5 mm
e

Fig. 7. *Termopsis bremii* (Heer) (AMNH C88891). **a**: Base of forewing. **b**: Left metatarsus and metatibial apex, oblique ventral view. **c**: Left metatarsus and metatibial apex, dorsal view. **d**: Dorsal view of head and pronotum. **e**: Ventral view of apex of abdomen.

Genus *Archotermopsis* Desneux, 1904

1904b *Termopsis (Archotermopsis)*. – Desneux, p. 13. Type species: *Termopsis (Archotermopsis) wroughteni* Desneux, 1904b, by monotypy.

Material examined: We have not had the opportunity to personally examine *A. tornquisti.*

Comments. – *Archotermopsis* is a primitive genus of termopsine termites known from two modern species, one living in the Himalayan Region of India and Pakistan as well as northeastern Afghanistan, the other in Vietnam. In addition, there is a single fossil species in Baltic amber, *A. tornquisti* (ROSEN 1913). This distribution, with living species in Asia and extinct taxa in the Paleocene-Eocene of Europe, is a relatively commonly observed biogeographic pattern. The genus can be recognized in the imago caste by the cryptically pentamerous metatarsus; the large compound eyes, with their conspicuously concave anterior margin (near the antennal articulation); antennae with 18–19 articles (23–27 articles in living species); the narrow pronotum, with its lateral borders distinctly converging posteriorly, and with the anterior and posterior borders emarginate; the tibial spur formula of 4-3-2 or 4-4-2 (based on living species); the tibiae of all legs with additional spines (varying from 1–6 in living species); the presence of the arolium; the straight and rather weak basal suture; and the elongate cerci (greatly surpassing the abdominal apex) with 6–8 long articles.

Family Kalotermitidae FROGGATT, 1897

Genus *Proelectrotermes* ROSEN, 1913

1913 *Calotermes (Proelectrotermes).* – ROSEN, p. 331. Type species: *Termes (Kalotermes) berendtii* PICTET-BARABAN in PICTET-BARABAN & HAGEN, 1856, by monotypy.

1941 *Calotermes (Neotermites).* – ARMBRUSTER, p. 18. Type species: *Calotermes (Neotermites) roseni* ARMBRUSTER, 1941, by original designation.

Material examined: One of us (K. K.) has examined a specimen of *P. berendtii* in the collection of the Chicago Natural History Museum and designated it as the neotype (KRISHNA 1961).

Comments. – The genus *Proelectrotermes* was originally established by ROSEN (1913) as an extinct subgenus of *Kalotermes*, at that time encompassing all kalotermitids. The group was later elevated to generic rank by EMERSON (1942) and combined with *Neotermites* by EMERSON (1971). Since that time the genus has been employed for the middle Eocene, Baltic amber species *P. berendtii* as well as two Tertiary compressions, *P. fodinae* (SCUDDER) from the Eocene-Oligocene boundary of Florissant, Colorado and *P. roseni* (ARMBRUSTER) from the Miocene Randeck Maar near Stuttgart, Germany, and, most recently, two species in mid-Cretaceous amber from Myanmar (ENGEL et al. 2007). KRISHNA (1961) and EMERSON (1969) have provided the most recent, detailed diagnoses for *Proelectrotermes*, recognizing the genus as encompassing primitive kalotermitids with at least three tibial spurs, with two outer spines and a single inner, subapical spine on the mesotibia. In addition, the radial field of *Proelectrotermes* is relatively broad in comparison to other kalotermitids and the radial vein is simple and elongate, extending near to the wing's midlength.

Genus *Electrotermes* Rosen, 1913

1913 *Calotermes (Electrotermes).* – Rosen, p. 331. Type species: *Termes affinis* Hagen in Pictet-Baraban & Hagen, 1856, by original designation.

Material examined: Two imagoes; AMNH B-E-2; AMNH B-E-5 (Fig. 8); middle Eocene (Lutetian), "Blaue Erde" deposit, Baltic amber.

Comments. – Like *Proelectrotermes*, the genus *Electrotermes* was originally established as a subgenus in *Kalotermes* before being elevated to generic rank by Emerson (1942). The genus is similar to *Proelectrotermes* except that the radial field is slightly narrower, the number of antennal articles is 14–18 (versus 19–20 in *Proelectrotermes*), the claval fissure (CuP) terminates prior to the basal suture (terminating at the posterior edge of the basal suture in *Proelectrotermes*), and the inner, subapical spine of the mesotibia is absent (only the two outer mesotibial spines are present).

Three species have generally been recognized in *Electrotermes* – two in Baltic amber, *E. affinis* (Hagen) (Fig. 8) and *E. girardi* (Giebel), and one in contemporaneous Parisian amber, *E. flecki* Nel & Bourguet. The two taxa in Baltic amber differ solely in forewing length with the scale (6 mm in *E. girardi* versus 8.84–8.94 mm in *E. affinis*). Hagen (1858) considered *E. girardi* a synonym of *E. affinis*, and various authors have considered the validity of the former as suspicious (e. g., Emerson 1969). Like Emerson (1969) we have tentatively retained *E. girardi* as a valid species and hopefully continued exploration of Baltic amber inclusions will bring further material to light.

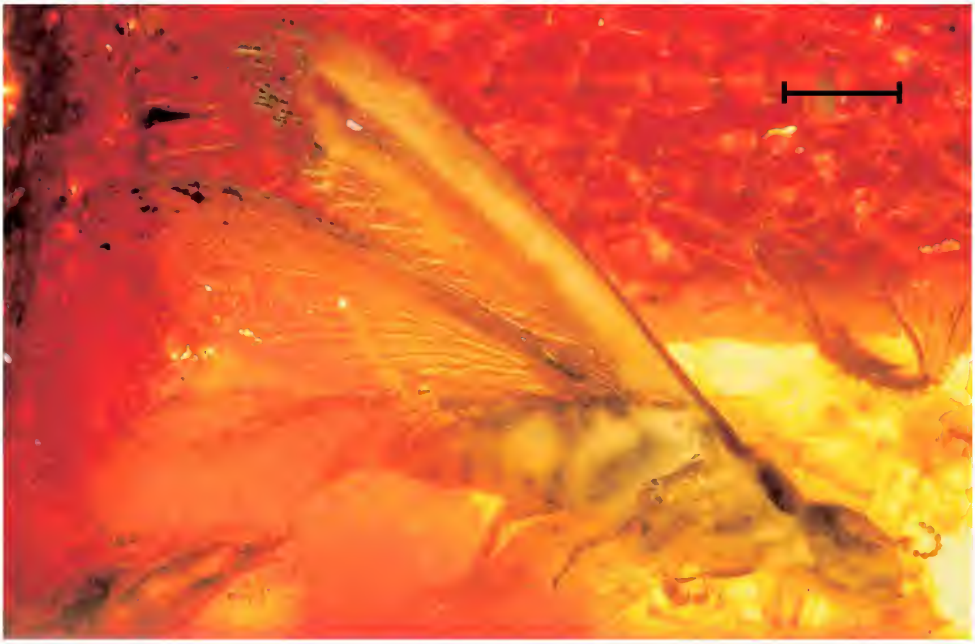

Fig. 8. Imago of *E. affinis* (specimen originally from the collection of Kurt von Rosen, donated by Rosen to Alfred E. Emerson in 1927) (AMNH B-E-5). – Scale bar = 1 mm.

Family Rhinotermitidae FROGGATT, 1897

Genus *Reticulitermes* HOLMGREN, 1913

1813 *Hemerobites.* – GERMAR, p. 16. Type species: *Hemerobites antiquus* GERMAR, 1813, by monotypy. Nomen oblitum (vide Comments, infra).

1856 *Maresa.* – GIEBEL, p. 298. Type species: *Maresa plebeja* GIEBEL, 1856, by monotypy. Nomen rejiciendum (vide Comments, infra).

1913 *Leucotermes (Reticulitermes).* – HOLMGREN, p. 60. Type species: *Termes flavipes* KOLLAR, 1837, by original designation. Nomen protectum.

1977 *Reticulitermes (Frontotermes).* – TSAI et al., p. 465. Type species: *Reticulitermes chinensis* SNYDER, 1923, by original designation.

1977 *Reticulitermes (Planifrontotermes).* – TSAI et al., p. 465. Type species: *Termes speratus* KOLBE, 1885, by original designation.

1983 *Tsaitermes.* – LI & PING, p. 239. Type species: *Reticulitermes (Planifrontotermes) yingdeensis* TSAI & LI in TSAI et al., 1977, by original designation.

Material examined: Eight imagoes of *R. antiquus*; AMNH B-JWJ-359 (specimen figured in JANZEN 2002: fig. 155); AMNH B-E-3; AMNH B-E-4; AMNH B-E-6 (Fig. 9a); AMNH C88891-B; AMNH B-JH-Iso1 (Fig. 9b); AMNH B-JH-Iso3; AMNH B-JH-Iso5; middle Eocene (Lutetian), "Blaue Erde" deposit, Baltic amber.

Comments. – The genus *Reticulitermes* is today widespread with 143 modern species. Various fossil species have been described, mostly as compressions, with two species documented in Baltic amber – *Reticulitermes antiquus* (GERMAR) and *R. minimus* SNYDER, both redescribed in detail by EMERSON (1971). *Reticulitermes antiquus* is the most common termite in Baltic amber (Fig. 9) and *R. minimus* is the smallest known termite (SNYDER 1928). *R. antiquus* can be distinguished most readily from *R. minimus* by its larger body size (length of forewing from basal suture 6.5–8.8 mm in *R. antiquus* versus 3.94 mm in *R. minimus*) and more numerous antennal articles (17–20 in *R. antiquus* versus 13–14 in *R. minimus*), among other characters (vide etiam Key, supra).

The genus-group name *Hemerobites* has priority over *Reticulitermes* (vide supra) but this name has not been used as valid after 1899 and literally hundreds of articles by dozens of authorities have employed the name *Reticulitermes* for these ubiquitous and economically important termites that are significant pests throughout the world. In accordance with ICZN (1999) Art. 23.9.1 we hereby consider *Hemerobites* as a nomen oblitum and *Reticulitermes* as a nomen protectum, automatically suppressing the former for purposes of priority whenever these two genera are considered synonyms (vide etiam ENGEL & KRISHNA in press).

The genus-group name *Maresa* similarly has priority over *Reticulitermes* (vide supra) and has been used only a couple of times as a valid taxon. Unfortunately, the last usage of the name was by HANDLIRSCH (1907), thereby rendering ICZN (1999) Art. 23.9.1 unusable for the conservation of *Reticulitermes*. We have, therefore, prepared a petition to suppress *Maresa* as a nomen rejiciendum for the purposes of priority (ENGEL & KRISHNA in press). In accordance with the ICZN (1999) current usage (i. e., with *Reticulitermes* as the valid generic name) must be maintained until a decision has been rendered by the Commission.

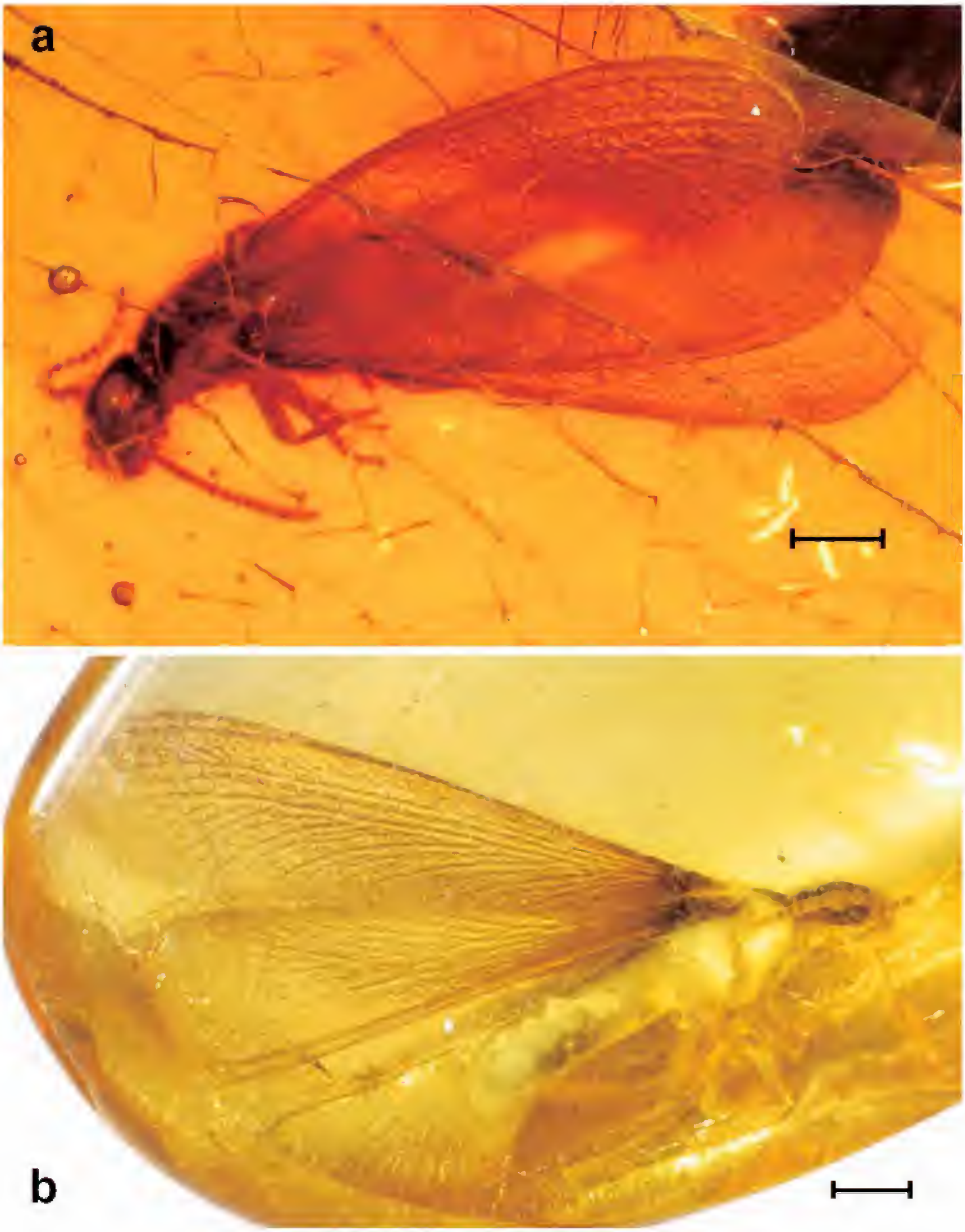

Fig. 9. Imagoes of *Reticulitermes antiquus* (Germar). **a**: Specimen originally from the collection of Kurt von Rosen (donated by Rosen to Alfred E. Emerson in 1927) (AMNH B-E-6). **b**: More recently excavated and identified specimen (AMNH B-JH-Iso1). – Scale bars = 1 mm.

Genus *Parastylotermes* Snyder & Emerson, 1949

1949 *Parastylotermes.* – Snyder & Emerson in Snyder, p. 378. Type species: *Stylotermes washingtonensis* Snyder, 1931, by original designation.

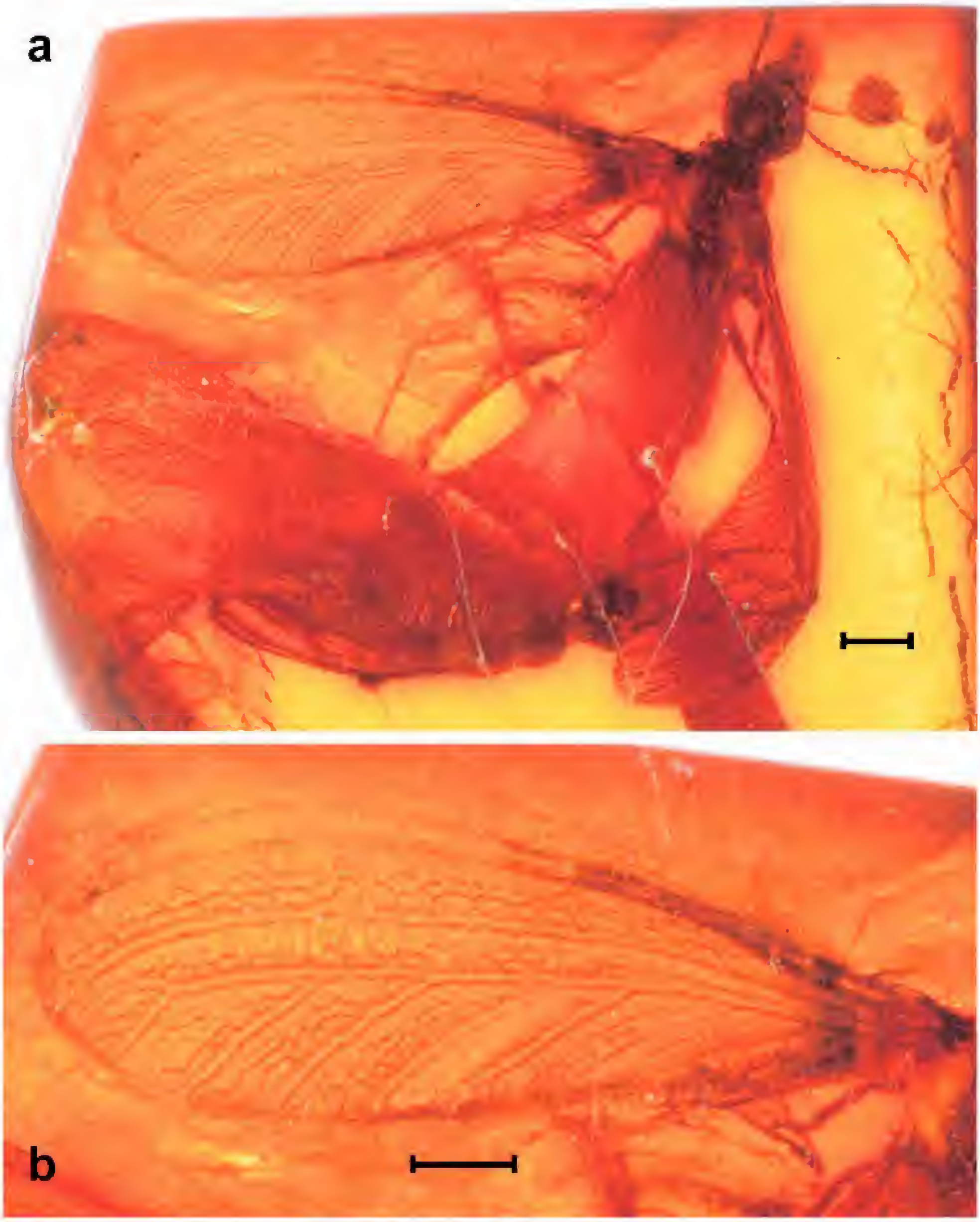

Fig. 10. Imagoes of *Parastylotermes robustus* (Rosen). **a**: Photomicrograph of lectotype and paralectotype imagoes (syntype specimens originally from the collection of Kurt von Rosen, donated by Rosen to Alfred E. Emerson in 1927) (AMNH B-E-7), uppermost specimen with wings spread is the lectotype selected by Emerson (1971). **b**: Forewing detail of lectotype. – Scale bars = 1 mm.

Material examined: Lectotype and paralectotype imagoes of *P. robustus* (Fig. 10); AMNH B-E-7; middle Eocene (Lutetian), “Blaue Erde” deposit, Baltic amber; lectotype and paralectotype designated by Emerson (1971).

Comments. – *Parastylotermes* was established for a Miocene species from the Latah Formation (State of Washington, USA) and for a single Baltic amber species previously placed in *Reticulitermes* (Snyder 1949). Two additional species from the Miocene of California were subsequently added by Snyder (1955) and Pierce (1958). The species from the Neogene of western North America are all known as compressions, with *Parastylotermes robustus* (Rosen) the sole amber representative of the genus (Fig. 10). It is unclear whether or not the Baltic amber species is truly congeneric with the North American taxa. The differences between the subfamilies Heterotermitinae and Stylotermitinae, and between *Stylotermes* and *Parastylotermes*, are subtle and largely quantitative. As such, the Paleogene *P. robustus* might rightfully belong in a genus distinct from the younger North American fossils. Unfortunately, the compressions do not afford fine enough detail to permit such discernment and *P. robustus* is most prudently retained in *Parastylotermes* despite the temporal separation and apparently peculiar disjunct distribution of the included species. *Parastylotermes* can be distinguished from the other rhinotermitids in Baltic amber by the more numerous and long setae of the head and pronotum (the individual setae are as long as or longer than the scape) and the pronotum distinctly narrower than the head.

3. Discussion

It is interesting to note that the Baltic amber termite fauna consists almost exclusively of primitive isopterans. *Garmitermes*, *Termopsis*, *Archotermopsis*, *Electrotermes*, and *Proelectrotermes* are all representative of primitive lineages. Only *Reticulitermes* and *Parastylotermes* are representative of the "higher" termites and therein only of the Rhinotermitidae. The today ubiquitous Termitidae are unknown from the Baltic amber fauna. Certainly termitids must have been present as evidenced by the occurrence of their sister group, the Rhinotermitidae. However, the family was apparently not even remotely as abundant as they are today and were, perhaps, represented during the latest Cretaceous and Early Tertiary merely by stem-groups, unassignable to modern subfamilies.

The distribution of the various taxa represented in Baltic amber is also most interesting. Many genera are wholly extinct (e. g., *Garmitermes*, *Termopsis*, *Electrotermes*, *Proelectrotermes*, and *Parastylotermes*) but have affinities to lineages today not occurring in Europe. *Garmitermes* is allied to the genus *Mastotermes*, a lineage that today consists of a single species restricted to Australia, but whose distribution included at least North America and Europe during the Tertiary and latest Cretaceous. *Termopsis* appears to have been entirely restricted to Europe, with species surviving through to the Miocene before eventually becoming extinct. The kalotermitid genera *Electrotermes* and *Proelectrotermes* are apparently related to a clade principally comprising Oriental genera, but also, in a more derived position of that same lineage, some widespread taxa also encompassing the African and Neotropical regions. Interestingly, while *Electrotermes* is confined to the Tertiary of Europe, *Proelectrotermes* encompasses two fossil species from the mid-Cretaceous of Myanmar in addition to a compression fossil species from the Miocene of Europe, the latter representing the last occurrence of the genus. A single species from the Eocene-Oligocene boundary of North America has also been included in *Proelectrotermes* but this species is represented solely by a fragmentary compression and its placement within *Proelectrotermes* may be erroneous. Similarly, *Parastylotermes* has been considered to encompass a Baltic amber species as well as two Miocene species from western North America. The North American compressions, however, are difficult to assign as the subtle characters of the Stylotermitinae are challenging to observe with great detail in minute compressions and this enigmatic, northern disjunct distribution may be an artifact (vide supra).

The remaining two genera, *Reticulitermes* and *Archotermopsis*, are both found in the modern fauna. *Reticulitermes*, the infamous subterranean termites so destructive to human habitation, is a remarkably diverse Holarctic genus. Relationships among the 143 currently recognized species, however, are unclear and it is unknown whether the species occurring in Baltic amber are allied to species today living in Asia or elsewhere. *Archotermopsis*, on the other hand, today consists of two species living in Asia, one in the Himalayan Region and the other in Vietnam. Such a connection between the Eocene fauna of Europe and modern taxa in Asia is a common biogeographic pattern seen for Baltic amber fossils (e.g., ANDER 1942; LARSSON 1978; ENGEL 2001).

4. References

ANDER, K. (1942): Die Insektenfauna des baltischen Bernsteins nebst damit verknüpften zoogeographischen Problemen. – Lunds Universitets Årsskrift, 2 Afdelning, Medicin samt Matematiska och Naturvetenskapliga Ämnen, **38**: 1–83.

ARMBRUSTER, L. (1941): Über Insektenstaaten der Vorwelt. 1. Miocäne Randecker Termiten. – Archiv für Bienenkunde, **22**: 3–43.

DESNEUX, J. (1904a): A propos de la phylogénie des Termitides. – Annales de la Société Entomologique de Belgique, **48** (8): 278–286.

DESNEUX, J. (1904b): A new termite from India. – Journal of the Bombay Natural History Society, **15**: 445–446.

EMERSON, A. E. (1933): A revision of the genera of fossil and Recent Termopsinae (Isoptera). – University of California Publications in Entomology, **6** (6): 165–196.

EMERSON, A. E. (1942): The relations of a relict South African termite (Isoptera, Hodotermitidae, *Stolotermes*). – American Museum Novitates, **1187**: 1–12.

EMERSON, A. E. (1969): A revision of the Tertiary fossil species of the Kalotermitidae (Isoptera). – American Museum Novitates, **2359**: 1–57.

EMERSON, A. E. (1971): Tertiary fossil species of the Rhinotermitidae (Isoptera), phylogeny of genera, and reciprocal phylogeny of associated Flagellata (Protozoa) and the Staphylinidae (Coleoptera). – Bulletin of the American Museum of Natural History, **146** (3): 243–304.

ENGEL, M. S. (2001): A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). – Bulletin of the American Museum of Natural History, **259**: 1–192.

ENGEL, M. S. & KRISHNA, K. (2004a): Family-group names for termites (Isoptera). – American Museum Novitates, **3432**: 1–9.

ENGEL, M. S. & KRISHNA, K. (2004b): An overlooked family-group name for termites (Isoptera). – Entomological News, **115** (3): 168.

ENGEL, M. S. & KRISHNA, K. (2007): Two overlooked family-group names for fossil termites (Isoptera: Mastotermitidae). – Entomological News, **118** (1): 105–106.

ENGEL, M. S. & KRISHNA, K. (in press): Case 3412: *Reticulitermes* HOLMGREN, 1913 (Insecta, Isoptera): Proposed conservation. – Bulletin of Zoological Nomenclature.

ENGEL, M. S., GRIMALDI, D. A. & KRISHNA, K. (2007): Primitive termites from the Early Cretaceous of Asia (Isoptera). – Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie), **371**: 1–32.

Froggatt, W. W. (1897): Australian Termitidae, Part II. – Proceedings of the Linnean Society of New South Wales, 21 (4): 510–552.

Germar, G. F. (1813): Insecten in Bernstein eingeschlossen, beschrieben aus dem academischen Mineralien-Cabinet zu Halle. – Magazin der Entomologie, **1**: 11–18.

Giebel, C. G. (1856): Fauna der Vorwelt mit Berücksichtigung der lebenden Thiere. Zweiter Band: Gliederthiere. Erste Abtheilung: Insecten und Spinnen. Die Insecten und Spinnen der Vorwelt mit steter Berücksichtigung der lebenden Insecten und Spinnen. xviii+511 pp.; Leipzig (F. A. Brockhaus).

Grimaldi, D. & Engel, M. S. (2005): Evolution of the Insects. xv+755 pp.; Cambridge (Cambridge University Press).

Hagen, H. A. (1858): Monographie der Termiten. – Linnaea Entomologica, **12**: i–iii, 4–342+459.

Handlirsch, A. (1907): Die fossilen Insekten und die Phylogenie der rezenten Formen: Ein Handbuch für Paläontologen und Zoologen. p. 641–1120, pl. 37–51; Leipzig (W. Engelmann).

Heer, O. (1849): Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien: Zweiter Theil: Heuschrecken, Florfliegen, Aderflügler, Schmetterlinge und Fliegen. iv+264 pp.; Leipzig (W. Engelmann).

Holmgren, N. (1911): Termitenstudien: 2. Systematik der Termiten. Die Familien Mastotermitidae, Protermitidae und Mesotermitidae. – Kungliga Svenska Vetenskaps-Akademiens Handlingar, **46** (6): 1–86.

Holmgren, N. (1913): Termitenstudien. 4. Versuch einer systematischen Monographie der Termiten der orientalischen Region. – Kungliga Svenska Vetenskaps-Akademiens Handlingar, **50** (2): 1–276.

International Commission on Zoological Nomenclature (1999): International Code of Zoological Nomenclature. xxix+306 pp.; London (International Trust for Zoological Nomenclature).

International Commission on Zoological Nomenclature (2005): Opinion 2124: Termopsidae Holmgren, 1911, *Termopsis* Heer, 1849 and *Miotermes* Rosen, 1913 (Insecta, Isoptera): Usage conserved by the designation of *Termopsis bremii* Heer, 1849 as the type species of *Termopsis* and the family-group name Termopsidae given precedence over Stolotermitinae Holmgren, 1910. – Bulletin of Zoological Nomenclature, **62** (3): 164–166.

Janzen, J.-W. (2002): Arthropods in Baltic Amber. 167 pp.; Halle (Ampyx-Verlag).

Keilbach, R. (1982): Bibliographie und Liste der Arten tierischer Einschlüsse in fossilen Harzen sowie ihrer Aufbewahrungsorte, Teil 1. – Deutsche Entomologische Zeitschrift, **29** (1–3): 129–286.

Kolbe, H. J. (1885): Zur Naturgeschichte der Termiten Japans. – Berliner Entomologische Zeitschrift, **29**: 145–150.

Kollar, V. (1837): Naturgeschichte der schädlichen Insekten. – Verhandlungen der Kaiserlich-Königlichen Landwirthschafts-Gesellschaft in Wien, N. F., **5**: 411–413.

Krishna, K. (1961): A generic revision and phylogenetic study of the family Kalotermitidae (Isoptera). – Bulletin of the American Museum of Natural History, 122 (4): 303–408.

Larsson, S. G. (1978): Baltic amber – A paleobiological study. – Entomonograph, **1**: 1–192.

Li, G.-X. & Ping, Z.-M. (1983): Description of a new genus *Tsaitermes* and its three new species from China (Isoptera: Rhinotermitidae: Heterotermitinae). – Entomotaxonomia, **5** (3): 239–245. [In Chinese, with English summary]

Nel, A. & Bourget, E. (2006): Termite [sic] of the Early Eocene amber of France (Isoptera: Mastotermitidae, Kalotermitidae). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **2006**: 101–115.

Pictet-Baraban, F.-J. & Hagen, H. A. (1856): Die im Bernstein befindlichen Neuropteren der Vorwelt. – In: Berendt, G. C. (ed.): Die im Bernstein befindlichen organischen Reste der Vorwelt [volume 2]: 41–126; Berlin (Nicolaische Buchhandlung).

Pierce, W. D. (1958): Fossil arthropods of California, No. 21: Termites from Calico Mountains nodules. – Bulletin of the Southern California Academy of Sciences, **57** (1): 13–24.

Rosen, K. von (1913): Die fossilen Termiten: Eine kurze Zusammenfassung der bis jetzt bekannten Funde. – In: Jordan, K. & Eltringham, H. (eds.): Transactions of the 2nd International Congress of Entomology [volume II]: 318–335; London (Hazell, Watson, and Viney).

SNYDER, T. E. (1923): A new *Reticulitermes* from the Orient. – Journal of the Washington Academy of Sciences, **13** (6): 107–109.

SNYDER, T. E. (1928): A new *Reticulitermes* from Baltic sea amber (Insecta – Isoptera). – Journal of the Washington Academy of Sciences, **18** (19): 515–517.

SNYDER, T. E. (1931): Insects from the Miocene (Latah) of Washington. IV. Isoptera. – Annals of the Entomological Society of America, **24**: 317.

SNYDER, T. E. (1949): Catalog of the termites (Isoptera) of the world. – Smithsonian Miscellaneous Collections, **112**: 1–490.

SNYDER, T. E. (1955): A new fossil termite *(Parastylotermes frazieri)* from California (Isoptera, Rhinotermitidae). – Proceedings of the Entomological Society of Washington, **57** (2): 79–80.

SPAHR, U. (1992): Ergänzungen und Berichtigungen zu R. KEILBACHS Bibliographie und Liste der Bernsteinfossilien – Klasse Insecta [Ausgenommen: "Apterygota", Hemipteroidea, Coleoptera, Hymenoptera, Mecopteroidea]. – Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie), **182**: 1–102.

TSAI, P.-H, HUANG, F.-S. & LI, K.-S. (1977): Notes on the genus *Reticulitermes* (Isoptera) from China, with descriptions of new subgenera and new species. – Acta Entomologica Sinica, **20** (4): 465–475. [In Chinese, with English summary]

WAPPLER, T. & ENGEL, M. S. (2006): A new record of *Mastotermes* from the Eocene of Germany (Isoptera: Mastotermitidae). – Journal of Paleontology, **80** (2): 380–385.

WEIDNER, H. (1955): Die Bernstein-Termiten der Sammlung des Geologischen Staatsinstituts Hamburg. – Mitteilungen aus dem Geologischen Staatsinstitut in Hamburg, **24**: 55–74.

WEITSCHAT, W. & WICHARD, W. (2002): Atlas of Plants and Animals in Baltic Amber. 256 pp.; Munich (Friedrich Pfeil Verlag).

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Revision of the Middle Jurassic dimorphic ammonite genera *Strigoceras*/*Cadomoceras* (Strigoceratidae) and related forms

Günter Schweigert, Volker Dietze, Robert Baron Chandler
& Vasilii Mitta

> *Facies non omnibus una,*
> *nec diversa tamen.*
> Ovid, Metamorphoses

Abstract

We present a modern revision of the dimorphic ammonite pair *Strigoceras* Quenstedt, 1886/*Cadomoceras* Munier-Chalmas, 1892 from the Middle Jurassic. The stratigraphically oldest hitherto known chronospecies of *Strigoceras*, *S. praenuntium* (Buckman) appears in the Middle Aalenian as an extreme rarity. Records of the microconch genus *Cadomoceras* remain unknown from strata older than Early Bajocian, but otherwise its stratigraphical range corresponds well with that of the macroconchs. The genus probably became extinct in the Early Bathonian (Zigzag Zone). The youngest known *Strigoceras* is *S. callomoni* n. sp. described here from the Macrescens Subzone of the Early Bathonian. Another new strigoceratid species, *Granulochetoceras oppeliisculptum* n. sp., is recorded by a single specimen from the early Garantiana Zone of eastern Spain, representing an interesting phyletic link between *Strigoceras* Quenstedt, 1886 and *Granulochetoceras* Geyer, 1960. We include a brief review of the latter genus. By including *Granulochetoceras* in the Strigoceratidae the family would extend to the Late Kimmeridgian of the Late Jurassic.

The palaeogeographic distribution of *Strigoceras*/*Cadomoceras* is focussed on the western Tethyan Province, but some species also occur in the northern Pacific and its adjacent shelves. A benefit of this large area of distribution is that strigoceratids may be used to correlate distant locations, but this is partly hampered by the relatively wide range of variability within succeeding chronospecies and remarkably large variation in size of adult macroconchs.

Keywords: Ammonites, biostratigraphy, Strigoceratidae, *Strigoceras*, *Cadomoceras*, *Granulochetoceras*, dimorphism, taxonomy, palaeobiogeography, Jurassic.

Zusammenfassung

Über das dimorphe Ammonitenpaar *Strigoceras*/*Cadomoceras* aus dem Mittel-Jura wird eine ausführliche moderne Revision vorgelegt und dessen phylogenetische Entwicklung dargestellt. Die bislang älteste bekannte Chronospezies von *Strigoceras*, *S. praenuntium* (Buckman), tritt bereits im Mittel-Aalenium auf, wenngleich extrem selten. Zugehörige Mikroconche der Gattung *Cadomoceras* sind bisher zwar erst ab dem Bajocium nachgewiesen, doch stimmt deren stratigraphische Reichweite ansonsten mit derjenigen der Makroconche überein. Das Dimorphenpaar *Strigoceras/Cadomoceras* scheint im Verlauf des Unter-Bathonium (Zigzag-Zone) erloschen zu sein. Aus der Macrescens-Subzone des Unter-Bathonium wird mit *Strigoceras callomoni* n. sp. die bisher jüngste bekannte *Strigoceras*-Art beschrieben, mit der die Gattung vermutlich erlosch. In der frühen Garantiana-Zone leitet eine weitere, bisher nur in einem Einzelstück bekannte neue Strigoceratiden-Art, *Granulochetoceras oppeliisculptum* n. sp., zur Gattung *Granulochetoceras* Geyer, 1960 über. Wir schließen eine kurze Übersicht über diese Gattung an. Die stratigraphische Reichweite der Familie Strigoceratidae insgesamt erweitert sich dadurch bis in das Ober-Kimmeridgium des Ober-Jura.

Die paläobiogeographische Verbreitung von *Strigoceras/Cadomoceras* liegt überwiegend in der westlichen Tethys, aber auch im Nordpazifik und dessen Randmeeren treten vereinzelte Vertreter auf. Dadurch besitzt dieses Dimorphenpaar eine gewisse Bedeutung für weltweite Korrelationen, die allerdings durch die teilweise beträchtliche Variabilität der aufeinander folgenden Chronospezies wieder deutlich eingeschränkt wird. Bemerkenswert ist auch eine beachtliche Größenvariation bei adulten Makroconchen.

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1. Introduction

In 1886, Quenstedt tentatively proposed a new Middle Jurassic ammonite genus *Strigoceras*, which is characterized by spiral striation of the shell, lateral depressions or furrows, and a smooth, septicarinate keel. In a revision of the ammonite genus *Strigoceras* and related genus *Phlycticeras*, Scheurlen (1928) overlooked numerous new taxa introduced by Buckman (1924) that are affiliated to *Strigoceras*. This author's sample of *Strigoceras* was poor, low in number and did not extend over the known stratigraphical range of the genus. In the early part of the 20th century Buckman (1909–1930) designated numerous new taxa with brief descriptions. Almost all were unknown outside Britain until the ammonitologist L. F. Spath sent copies to the German authority O. H. Schindewolf. Arkell (1950) considered Strigoceratidae as of cryptogenic affiliation, possibly parallel with Oppeliidae. Later, Arkell (1957) synonymised several of Buckman's genera with *Strigoceras*.

The microconch genus *Cadomoceras* was introduced by Munier-Chalmas (1892: 171); it possesses an eccentric bodychamber and large lateral lappets. Munier-Chalmas was among the first scientists to recognize sexual dimorphism in ammonites, and the first to give some convincing examples of dimorphic pairs (Callomon 1963; Makowski 1963). The origin of *Cadomoceras* remained a mystery, even after a first revision of this genus by Coemme (1918). Dacqué (1934) included *Cadomoceras* into the oppeliids. Arkell (1957) retained *Cadomoceras* in the Haploceratidae Zittel, 1884, which at that time was a polyphyletic taxon in which micro- and macroconchs of various systematic affinities were lumped together.

The dimorphism between *Strigoceras* and the minute *Cadomoceras* was first observed by Sturani (1971). The striking resemblance between the inner whorls is obvious, but there were sound objections to disagree with this association (Dietl 1986) based on a long-lasting confusion between the two striate genera *Strigoceras* and *Phlycticeras*. There was also the erroneous assumption that *Phlycticeras* had evolved from *Strigoceras* (Callomon in Donovan et al. 1981). The dimorphism between *Phlycticeras* and *Oecoptychius* is well established, but for practical reasons we still distinguish the corresponding dimorphs taxonomically (Schweigert & Dietze 1998, 1999; Schweigert et al. 2003). The development of the suture line during early ontogeny was studied by Schindewolf (1964, fig. 205 *(Strigoceras)*, fig. 209 *(Cadomoceras)*). However, at that time dimorphism between both genera was not taken in consideration.

A brief phyletic overview, almost exclusively based on material from south-eastern Spain, was presented by Sandoval (1985). In his phyletic tree he separated two parallel lineages of strigoceratids, one leading to *Strigoceras truellei* (d'Orbigny), the other to *Strigoceras paronai* (Trauth). Following Arkell (1957) he also tentatively included *Hebetoxyites* Buckman, 1924 in Strigoceratidae, a primitive oppeliid genus known from the Lower Bajocian. Recently, Moyne & Neige (2004) proposed a phyletic relationship for *Praestrigites* within a hammatoceratoid ancestry based on a computer cladistic analysis that included very few morpho-genera, totally ignoring the dimorphism, which in our opinion is one of the most significant features.

In the present revision strigoceratid specimens from worldwide sources are included along with available types. There is special emphasis on the biostratigraphically well documented localities yielding strigoceratids from Submediterranean sections in England, SW Germany, and Central Spain.

Abbreviations

BGS	British Geological Survey, Keyworth, Nottingham, United Kingdom
BNHM	Natural History Museum, London, United Kingdom
BSPM	Bayerische Staatssammlung für Paläontologie und Geologie München, Germany
GBA	Geologische Bundesanstalt, Wien, Austria
GIUS	Geological Institute, Department of Ecosystem Stratigraphy, University of Silesia, Sosnowiec, Poland
IFGT	Institut für Geowissenschaften der Universität Tübingen, Germany
MNHN	Muséum Nationale d'Histoire naturelle, Paris, France
NHMB	Naturhistorisches Museum Basel, Switzerland
RBC	Robert Baron Chandler Collection, Whyte Leafe, Surrey, United Kingdom
SM	Sedgwick Museum, Cambridge, United Kingdom
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany
VNIGNI	All-Russia Research Geological Oil Institute Moscow, Russia
[M]	ammonite macroconch dimorph
[m]	ammonite microconch dimorph
d	diameter [mm]
h	height of last whorl [mm]
u	width of umbilicus [mm]
w	width of last whorl [mm]
r/2	secondary and tertiary ribs per half a whorl

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2. Palaeobiogeographic distribution of *Strigoceras/Cadomoceras*

The Middle Jurassic ammonite genus *Strigoceras* and/or its microconch partner *Cadomoceras* is recorded from the following regions (specimens not determined as strigoceratids by the original authors are included here, but erroneous citations are omitted):

Belgium: Maubeuge (1951).

France (extraalpine part): Defrance (1830); Blainville (1840); d'Orbigny (1845); Bayle (1878); Douvillé (1884); Quenstedt (1886); Brasil (1895); Fischer (1994); Lissajous (1906, 1907–1912); Coemme (1918); Wetzel (1924); Scheurlen (1928); Roché (1939); Mouterde (1953); Doré et al. (1987); Gauthier et al. (1995, 2002); Rioult (1964, 1971); Rioult et al. (1997); Fernández López & Mouterde (1994a, 1994b); Rulleau (1997); Elmi & Rulleau (1993); Thierry et al. (1997); Richter (2003); Rulleau (2006); this study.

Germany (southern part): Oppel (1856); Quenstedt (1886); Engel (1908); Scheurlen (1928); Dietl (1977); Dietl & Rieber (1980); Wittmann (1983); Schatz (1985); Schlegelmilch (1985); Gassmann & Ohmert (1990); Hegele (1990, 1995); Ohmert (1988, 1990); Ohmert et al. (1995); Schlampp (1997); Schweigert & Dietze (1999); Arp (2001); Dietze et al. (2002, 2004); Schweigert et al. (2002); this study.

Germany (northern part): Kumm (1952); Westermann (1958); Huf (1968); this study.

England: Wright (1860); Buckman (1893, 1910, 1923, 1924); Arkell (1933); Wilson et al. (1958); Torrens (1969); Whicher (1969); Senior et al. (1970); Whicher & Palmer (1971); Morton (1975, 1976); Parsons (1974, 1975, 1976, 1977, 1979); Callomon & Chandler (1990, 1994); Callomon & Cope (1995); Huxtable (1991, 2000, 2006); Cox & Sumbler (2002); Chandler & Dietze (2001, 2003); Chandler et al. (2006); Dietze et al. (2007); this study.

Poland (extracarpathian part): Zatoń & Marynowski (2004, 2006); this study.

Portugal: Rocha et al. (1990); Mouterde (1991).

Spain and Baleares: Fallot & Blanchet (1923); Westermann (1955); Mensink (1965); Hinkelbein (1975); Sequeiros et al. (1978); Fernández López (1977, 1982, 1985, 1988); Fernández López & Aurell (1988); Fernández López & Gómez (1990); Fernández López & Suárez-Vega (1979); Fernández López et al. (1988, 1997, 1998); Sandoval (1979, 1985, 1986, 1990, 1994); Alvaro et al. (1989); Linares & Sandoval (1979, 1990, 1993); this study.

Switzerland: Ooster (1860); Scheurlen (1928); Bircher (1935); Maubeuge (1955); Dollfuss (1961); this study.

Austria (Eastern Alps): Trauth (1923a, 1923b, 1928); Krystyn (1971, 1972).

France (French part of Western Alps): Haug (1891); Lanquine (1929); Pavia & Sturani (1968); Pavia (1969, 1973).

Italy (Southern Alps): Parona (1896); Sturani (1964a, 1964b, 1971); Benetti (1977); Della Bruna & Martire (1985).

Italy (Apennines): Cresta (1988); Baldanza et al. (1990); Cresta & Galácz (1990); Cecca et al. (1991).

Italy (Sicily): Wendt (1963, 1971); D'Arpa in Pavia & Cresta (2002); Di Stefano et al. (2002); Santantonio (2002).

North Africa: Flamand (1911); Menchikoff (1936); Verlet & Roch (1940); Atrops (1974); Enay et al. (1987); Benhamou & Elmi (1994); Sadki (1994a, 1994b, 1996); Sadki et al. (1986).

Hungary: Galácz (1970, 1976, 1980, 1988, 1991).

Poland and Slovakia (Carpathians): Krobicki & Wierzbowski (2004); Schlögl (2002); Schlögl et al. (2005).

Caucasus and Turkmenistan: Arkell (1956); Krymholtz & Stankevitch (1963); Rostovtsev (1985); Rostovtsev (1992); Besnosov & Mitta (1998, 2000); this study.

Iran: Seyed-Emami (1988); Seyed-Emami & Alavi-Naini (1990).

Alaska: Imlay (1964); this study.

Canada: Hall & Westermann (1980); Poulton et al. (1992).

Oregon: Lupher (1941); Imlay (1973); Taylor (1988); Taylor & Smith (1991).

Mexico: Sandoval & Westermann (1986); Salvador et al. (1992).

Japan: Sato (1962, 1972); Sato & Westermann (1991).

In contrast to the morphologically similar and phylogenetically related dimorphs *Phlycticeras/Oecoptychius*, the genus *Strigoceras* and its anti-dimorph *Cadomoceras* has to date not been recorded from the Indo-East African Province nor from South America. A record of *Strigoceras* from Chile (Hillebrandt et al. 1997: 349) was erroneous (pers. comm. A. v. Hillebrandt) and referred to records of *Phlycticeras* from around the Bathonian/Callovian boundary (see Schweigert & Dietze 1998). The absence of *Strigoceras/Cadomoceras* in the Indo-East African Province is probably due to the scarcity of ammonite-bearing Middle Jurassic strata of pre-Bathonian age in this area. Strigoceratids are completely missing in Boreal or Subboreal faunas. *Liroxyites* Imlay, 1961 from the Bajocian of Alaska may be an endemic oppeliid genus with striking homoeomorphy with *Strigoceras* and *Hebetoxyites*.

Moyne et al. (2004) analyzed the palaeobiogeographic distribution of several Middle Jurassic ammonite subfamilies, including Strigoceratinae. Their data for Strigoceratinae fits well with ours, but is based on morphotaxa, not chronospecies; therefore their records tell us little about real abundance or specific diversity in an area.

The bulk of strigoceratids comes from the western Tethys. It is unclear if this region was also a centre of diversification or even origination for this family, in view of the general scarcity of stratigraphically early representatives of strigoceratids, and isolated discoveries in some north-Pacific terrains.

3. Systematics of the macroconch ammonite genus *Strigoceras*

The species concept adopted in this study follows Dietze et al. (2005). The phyletic lineage of a genus is built up as a succession of chronospecies, based on their identified and defined type horizons. Transitional morphs showing the plasticity of the shell parameters and the sculptural characteristics are treated as morphological variants below the subspecific level. We formally retain separate macro- and microconch taxa at both generic and specific level. In the extreme dimorphic associations we describe, microconchs have restricted morphological variability in contrast to macroconchs. Unification of corresponding, co-occurring micro- and macroconch taxa into a single (palaeo-)biospecies seems inappropriate here. Sometimes the known stratigraphical ranges of microconch morphospecies do not follow perfectly that of their presumed macroconch counterparts (Fig. 1). This is comparable to what is observed in closely related *Phlycticeras* [M]/*Oecoptychius* [m] (see Schweigert & Dietze 1998). Despite common usage we reject subgeneric ranking of corresponding dimorphs, not only for nomenclatorial reasons (see Pavia 2006) but because subgeneric placement should express (palaeo-)biogeographic or habitat differentiation within a genus.

Order Ammonoidea Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Haploceratoidea Zittel, 1884
Family Strigoceratidae Buckman, 1924
Subfamily Strigoceratinae Buckman, 1924

Genus *Strigoceras* Quenstedt, 1886 [M]
(Syn.: *Stringoceras* Douvillé, 1916; *Praestrigites* Buckman, 1924; *Deltostrigites* Buckman, 1924; *Leptostrigites* Buckman, 1924; *Plectostrigites* Buckman, 1924; *Strigites* Buckman, 1924; *Varistrigites* Buckman, 1924)

Type species: *Ammonites truellei* d'Orbigny, 1845.
Species included: *Praestrigites praenuntius* Buckman, 1924; *Strigites strigifer* Buckman, 1924; *Leptostrigites languidus* Buckman, 1924; *Strigoceras bessinum* Brasil, 1895; *Plectostrigites symplectus* Buckman, 1924; *Strigites septicarinatus* Buckman, 1924; *Ammonites truellei* d'Orbigny, 1845; *Strigoceras callomoni* n. sp. (this study). Other synonymous taxa are presented.

Diagnosis. – Medium-size ammonites with high-oval to oxyconic cross section, longitudinal spiral striation of the shell with one to four lateral depressions or furrows, very narrow umbilicus, rounded umbilical wall, falcoid or irregular polyschizotome ribbing and low, rounded, unsculptured septicarinate keel; aptychi unknown.

Age		Zone	Subzone	*Strigoceras*	*Cadomoceras*
BATH.	Early	Zigzag	Tenuiplicatus		
			Yeovilensis		
			Macrescens	*S. callomoni*	unknown
			Convergens		
BAJOCIAN	Late	Parkinsoni	Bomfordi		
			Truellei	*S. truellei*	*C. cadomense*
			Acris	*S. septicarinatum*	
		Garantiana	Tetragona		
			Garantiana		
			Dichotoma		
		Niortense	Baculata	*S. symplectum*	
			Polygyralis		*C. nepos*
			Banksii		
	Early	Humphriesianum	Blagdeni		
			Humphriesianum		
			Romani	*S. bessinum*	*C. sullyense*
		Sauzei	Hebridica	*S. languidum*	*C. carinatum*
			Patella		
		Laeviuscula	Laeviuscula	*S. strigifer*	*C. costellatum*
			Trigonalis		
		Ovale	Ovale	*S. compressum*	
		Discites	Subsectum		
			Walkeri		
AALENIAN	L.	Concavum	Formosum		
			Concavum		unknown
	Middle	Bradfordensis	Gigantea	*S. praenuntium*	
			Bradfordensis		
		Murchisonae	Murchisonae		
			Obtusiformis		
			Haugi		
	E.	Opalinum	Comptum		
			Opalinum		

Fig. 1. Biochronostratigraphy of the Aalenian to Early Bathonian, with zonal and subzonal subdivisions mentioned in the text. Times during which *Strigoceras* or *Cadomoceras* are recorded are indicated by grey colour.

Strigoceras praenuntium (BUCKMAN, 1924)

Figs. 2–3

v * 1924 *Praestrigites praenuntius*, nov. – BUCKMAN, pl. 466.
v 1924 *Deltostrigites deltotus*. – BUCKMAN, pl. 467.
v 1957 *Praestrigites praenuntius*. – ARKELL, p. L271.
1967 *Praestrigites praenuntius* BUCKMAN, 1924. – GÉCZY, p. 223, pl. 26, fig. 2, pl. 57, fig. 2.

? 1971 *Praestrigites praenuntius* Buckman, 1924. – Géczy, p. 415.
v 1971 *Strigoceras* sp. indet. – Wendt, p. 156.
1973 *Praestrigites* cf. *P. deltotus* (Buckman). – Imlay, p. 75, pl. 35, figs. 1–9, 11–14; p. 75, figs. 3–4.
1973 *Strigoceras* cf. *S. languidum* (Buckman). – Imlay, p. 76, pl. 36, figs. 13–21.
1976 *Strigoceras*. – Galácz, p. 180.
1983 *Praestrigites* sp. – Sandoval, p. 116, tab.-fig. 77a.
1983 *Strigoceras* sp. – Sandoval, p. 116.
? 1985 *Praestrigites deltotus* (Buckman, 1924). – Sandoval, p. 89, pl. 1, fig. 1.
1986 *Strigoceras* sp. – Sadki et al., p. 452.
1988 *Praestrigites*. – Cresta, tab.-fig. 3.
? 1988 *Praestrigites*. – Cresta, tab.-fig. 4.
? 1988 *Strigoceras*. – Cresta, tab.-fig. 4.
1988 *Praestrigites*. – Fernández López et al., text-figs. 2–3. – [1988c].
1988 *Strigoceras harrisense*. – Taylor, p. 135, pl. 3, figs. 4–5.
1990 *Praestrigites deltotus* (Buckman). – Baldanza et al., p. 226.
1990 *Strigoceras* sp. – Baldanza et al., p. 226.
1990 *Praestrigites* cfr. *praenuntius* Buckman. – Baldanza et al., p. 226.
1990 *Praestrigites deltotus* (Buckman). – Cresta & Galácz, pp. 168, 171, pl. 13, fig. 4, pl. 11, aff.-specimen text-fig. 1, pl. 2, fig. 2.
1990 *Praestrigites* sp. – Cresta & Galácz, pl. 10, fig. 2.
1990 *Praestrigites*. – Fernández López & Gomez, p. 47.
pars 1990 *Praestrigites* sp. – Rocha et al., pl. 1, fig. 4, tab.-fig. 2.
1990 *Strigoceras deltotus*. – Sandoval, p. 144.
1990 *Praestrigites deltotus*. – Linares & Sandoval, tab.-fig. 2.
v non 1990 *Praestrigites protrusus*. – Callomon & Chandler, p. 97 [comment see p. 49].
1991 *Praestrigites deltotus* Buckman. – Cecca et al., p. 92.
1991 *Praestrigites praenuntius* Buckman. – Cecca et al., p. 92.
1992 *Strigoceras harrisense* Taylor. – Poulton et al., p. 72, pl. 42, fig. 6.
1993 *Praestrigites* sp. – Linares & Sandoval, tab.-fig. 5.
? 1994 *Praestrigites*. – Sadki, pp. 315, 320. – [1994b].
1996 *Praestrigites*. – Sadki, pp. 48, 137, tab.-figs. 12–13, 30.
1997 *Praestrigites*. – Rioult et al., p. 46.
1997 *Strigoceras*. – Rioult et al., p. 46.
2002 *Praestrigites deltotus* Buckman. – Cresta et al. in Santantonio, p. 229.

Holotype: Specimen figured by Buckman 1924, pl. 466, BGS GSM 37314, refigured herein as Fig. 2.

Type locality: Horn Park, Beaminster, Dorset, England.

Type horizon: Inferior Oolite, Ironshot Bed ("Ludwigian, *platychora* hemera" of Buckman). An investigation of the specimen's matrix showed it to be ironshot and therefore later than bed 4 of Horn Park. By comparison of the matrix it probably comes from bed 5a (Middle Aalenian, Bradfordensis Zone, Gigantea Subzone, Aa-11, *gigantea* horizon, see Callomon 1995).

Studied material: 3 specimens.

Stratigraphic range: The stratigraphically oldest record of *Strigoceras praenuntium* (Buckman), if correctly identified, was from the late Opalinum Zone of Hungary (Géczy 1971). The preservation of ammonites in the Rosso Ammonitico lithology at Csernye makes it difficult to distinguish between early *Strigoceras* and co-occurring *Csernyeiceras*. It was impossible to trace a specimen in the collection of Budapest University labelled as "*Strigoceras praenuntium*" of this age, and most likely the reference is based on specimens from the Middle Aalenian earlier recognized and illustrated by Géczy (1967: 223, pl. 56, fig. 2, pl. 57, fig. 2, pl. 65, fig. 78; pers. comm. A. Galácz, Budapest). Therefore the oldest undoubted record is that

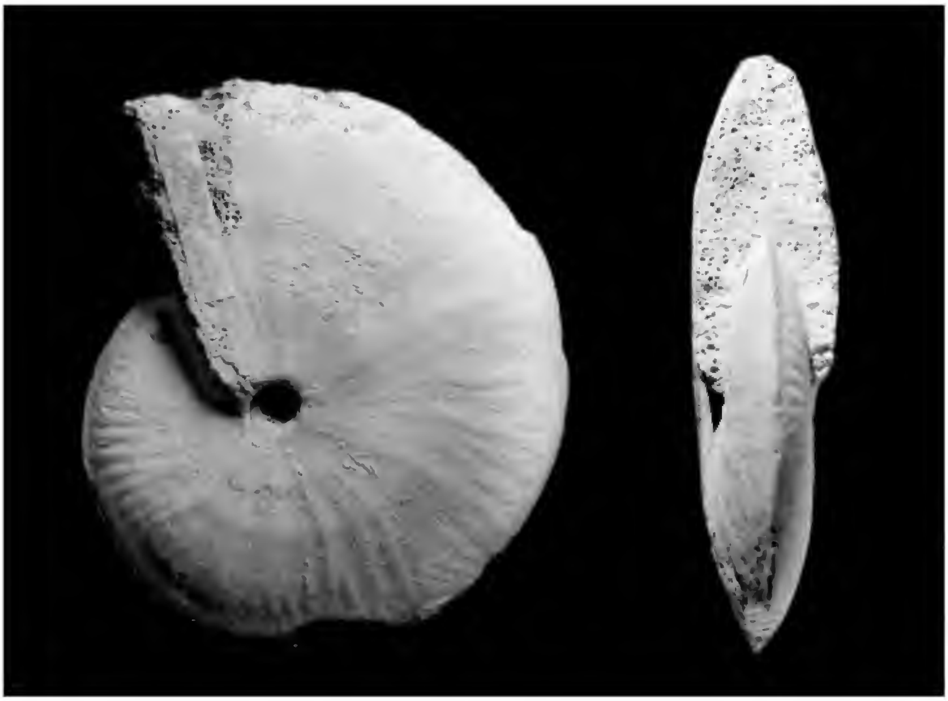


Fig. 2. *Strigoceras praenuntium* (BUCKMAN), holotype, lateral and ventral views; Horn Park; Inferior Oolite, bed 5a, Middle Aalenian, Bradfordensis Zone, *Brasilia gigantea* horizon (= horizon Aa-11 of CALLOMON 1995); BGS GSM 37314. – ×1.

of the holotype itself coming from the Middle Aalenian. Very rare specimens of *S. praenuntium* from the Concavum Zone are recorded from Spain, Portugal, Morocco, from the Apennines and Southern Alps, and from Hungary. Records from the Discites Zone come from England, France, Spain, Morocco, Apennines, Sicily, Hungary, and from Oregon. The latest known representatives of the morphospecies *S. praenuntium* are from the Discites Zone.

Records: England, Oregon, Spain, Portugal, Morocco, Apennines, Southern Alps, Hungary.

Diagnosis. – *Strigoceras* with a slender cross section, a weakly developed median lateral furrow, rectiradiate to rursiradiate, irregularly falcoid to polyschizotome ribbing.

Description. – The holotype is a complete phragmocone with a little body chamber in shell preservation. The original length of the bodychamber was about half a whorl, reconstructed from the length of the spur line. The shell is preserved in brown calcite. In the last third of one flank, the shell has been removed to study the extremely complex suture line. The cross section is oxyconic with its maximum width at mid-height of the flank. The septicarinate keel is low and rounded. A median lateral furrow is weakly developed and only discernible in specimens with the shell preserved. The ornament consists of rather dense falcoid/polyschizotome ribs with numerous irregular secondaries. The secondaries are generally rectiradiate, but in BUCKMAN's original figure they are painted in to show a prorsiradiate direction; this is misleading. In the latest stage of ribbing the ribs become coarse and more widely spaced. A longitudinal striation is developed but scarcely discernible due to the calcitic preservation of the shell. The umbilical wall is steep and the umbilical width very small; however it attains the largest value at equal diameter for the entire genus. In contrast to many other specimens of similar size, the suture line of the holotype of *S. praenuntium* appears relatively simple, but this feature is individual and means that the specimen was far from being adult.

Comparisons. – *Strigoceras praenuntium* differs from other slender chronospecies of the genus in possessing quite densely ribbed inner whorls, with ribs becoming irregular and polyschizotome early in ontogeny and rapidly coarsening towards maturity. In *S. bessinum* BRASIL similar morphology is seen, but with a more accentuated lateral furrow and stronger ribbing overall.

Remarks. – *Strigoceras praenuntium* was originally erected as type species of *Praestrigites* BUCKMAN, 1924. Unlike many other generic names introduced by BUCKMAN for strigoceratids of different ages, *Praestrigites* was accepted by ARKELL (1957) and, more recently SANDOVAL (1985) as a separate taxon. There is no doubt that it does have a close relationship with *Strigoceras* but the morphological differences between *Strigoceras* s. str. and *Praestrigites* cited in their emendations are a factor of the preservational state of the types of species included. The lateral median furrow is shallow and often only visible when the shell is preserved.

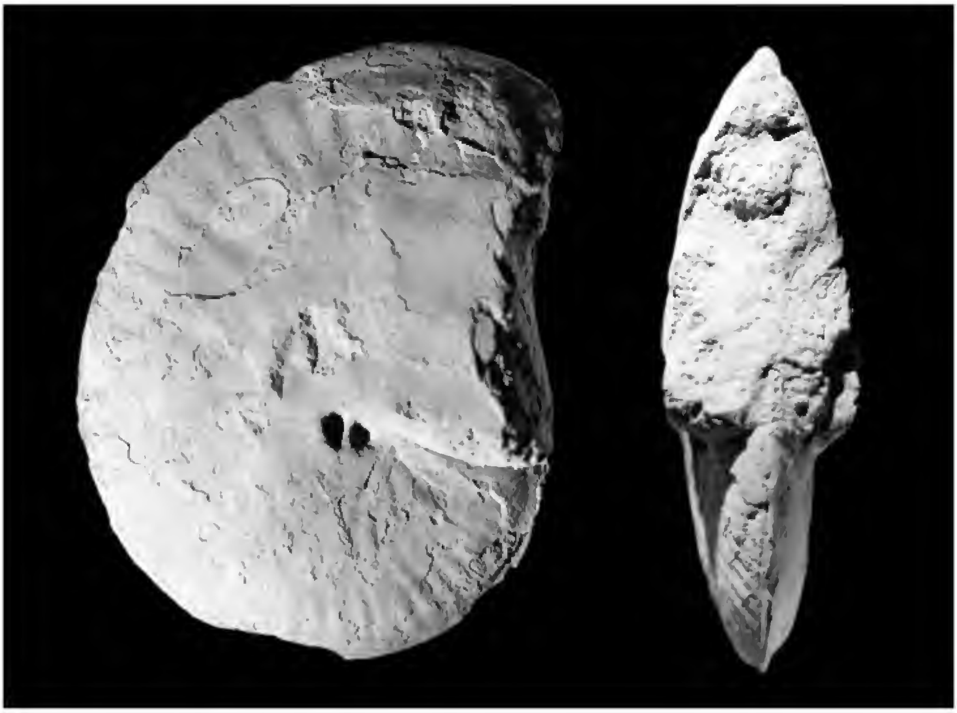


Fig. 3. *Strigoceras praenuntium* (BUCKMAN) (= holotype of *Deltostrigites deltotus* BUCKMAN), lateral and ventral views; Bradford Abbas; Inferior Oolite, Fossil Bed, Lower Bajocian, Discites Zone; BGS GSM 37315. – ×1.

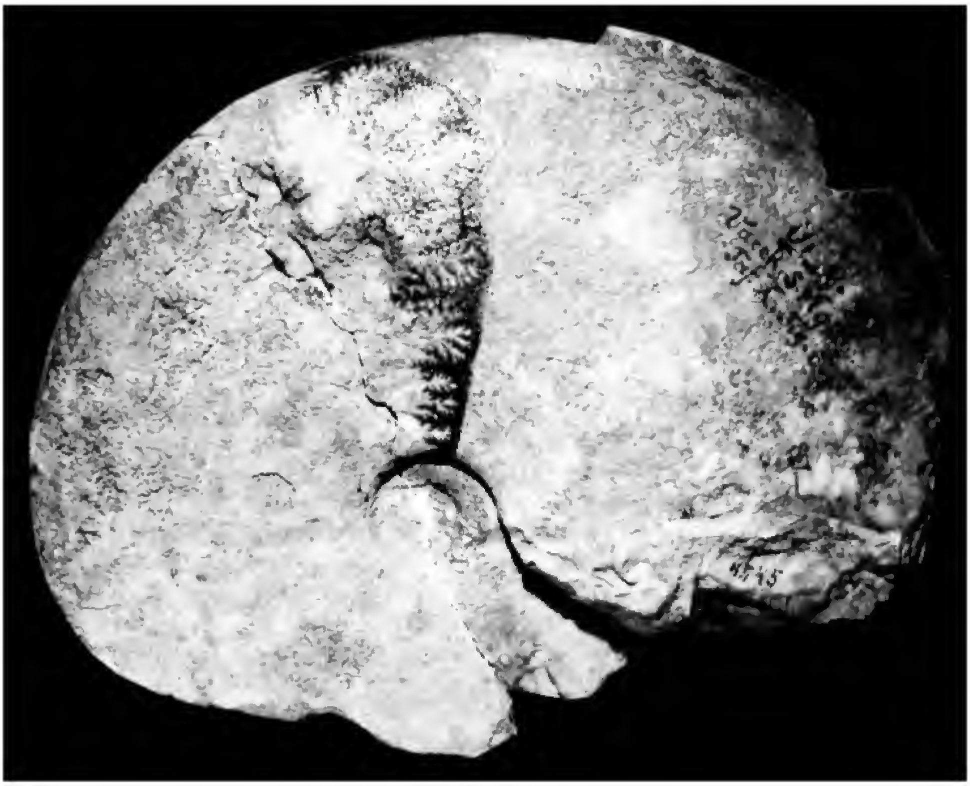


Fig. 4. *Csernyeiceras subaspidoides* (Vacek), syntype, lateral view; Cap San Vigilio, Lake Garda, N Italy; Aalenian,? Concavum Zone; GBA 1886/05/29a. – ×1.

The holotype of *Deltostrigites deltotus* Buckman (Fig. 3) is from the Discites Zone (Inferior Oolite, Fossil Bed) of Bradford Abbas. The distinction between *S. praenuntium* and *S. deltotum* made in literature is entirely based on the horizon of occurrence. There is little foundation for separating the two taxa on the analysis of their types by morphology or on the grounds of intraspecific variation (although number of specimens is still low). We prefer to include both in the same taxon.

Recent reinvestigation of all three syntypes of *Oppelia subaspidoides* Vacek, 1886, from the Aalenian of Cap San Vigilio proved them all to belong to *Csernyeiceras*, not to *Praestrigites* as recently suggested by Schweigert et al. (2000) for the remaining syntypes besides the lectotype. This determination is based on the extremely high, razor-sharp septicarinate keel, a relatively wide umbilicus, and the absence of any lateral furrows (see also p. 50; Fig. 4). The suture line, however, is hardly distinguishable from that of a *Strigoceras*, thus demonstrating the close phyletic relationship between Phlycticeratinae and Strigoceratinae. A specimen described as "*Oppelia* cfr. *subaspidoides* Vacek" by Prinz (1904, pl. 20, fig. 1) is more involute than any of the syntypes of *Oppelia subaspidoides*, but this specimen has an extraordinarily sharp keel and a cross section more typical of *Csernyeiceras* (Géczy 1967, pl. 56, fig. 1, text-fig. 236), although its rather poor preservation in Rosso Ammonitico lithology hampers any reliable comparison.

Measurements

	d	h	w	u	r/2	h/d	w/d	u/d
GSM 37314 (holotype)	(75.5)	(44)	18.5	4.8	~45	0.58	0.25	0.06
dito	65.0	38.0	15.0	4.3	35.0	0.58	0.23	0.07
GSM 37315 (Fig. 3)	83.5	51.0	23.3	2.0	~25	0.61	0.28	0.02

Strigoceras compressum BUCKMAN, 1896
Figs. 5–6

1896 *Strigoceras compressum* (ETHERIDGE). – BUCKMAN in BUCKMAN & WILSON, p. 701.
v * 1924 *Varistrigites compressus*, ETHERIDGE sp. – BUCKMAN, pl. 468.
1974 *Strigoceras compressum* (S. B.). – PARSONS, p. 169.
1977 *Strigoceras compressum* (S. B.). – PARSONS, p. 116.
1979 *Strigoceras (S.) compressum* (S. BUCKMAN). – PARSONS, p. 144.
1979 *Varistrigites compressus*. – PARSONS, p. 148, table 4.
1985 *Strigoceras compressum*. – DELLA BRUNA & MARTIRE, p. 42.
1985 *Strigoceras comprexum* (ETHERIDGE) sensu BUCKMAN 1924. – SANDOVAL, p. 93, pl. 1, figs. 2–3.
1988 *Strigoceras compressum*. – FERNÁNDEZ LÓPEZ et al., tab.-fig. 2.
1990 *Strigoceras compressum*. – SANDOVAL, p. 146.
v 2006 *Strigoceras compressum* (ETHERIDGE). – CHANDLER et al., tab.-fig. 2.
v 2007 *Strigoceras strigifer* (BUCKMAN). – DIETZE et al., p. 17, text-fig. 5a, b.
v 2007 *Strigoceras compressum* BUCKMAN. – DIETZE et al., p. 17, text-fig. 5c, d.

Taxonomic remarks. – *Ammonites truellei* var. *compressus* ETHERIDGE in WRIGHT (1860: 24) was erected without a figure, description or indication of any syntypes and its exact stratigraphical position within the Inferior Oolite is unknown. Originally the name was applied to various slender specimens coming from different stratigraphical horizons (BUCKMAN in BUCKMAN & WILSON 1896: 701), thus prior to BUCKMAN (1924), the taxon represents a nomen nudum. BUCKMAN (1924) emended the species to include a "large" form from his *fissilobatum* hemera retaining ETHERIDGE as author. The figured specimen is extremely coarse-ribbed (BUCKMAN 1924, pl. 468), and was referred to as a "topotype". It is the only strigoceratid from S. S. BUCKMAN's 'Type Ammonites' that could not be located in the palaeontological collections of BGS. The specimen from J. W. TUTCHER's collection is now in the Natural History Museum, London (communication by J. H. CALLOMON). It has been impossible to define an original type series at disposal by BUCKMAN in 1896. The specimen illustrated here (Fig. 5) from the TUTCHER collection was recently erected as neotype, characteristic of the species (DIETZE et al. 2007).

Neotype: Specimen figured by BUCKMAN 1924, pl. 468, designated by DIETZE et al. (2007), BNHM C.41727, re-figured here as Fig. 5.

Type locality: Dundry Hill near Bristol.

Type horizon: Inferior Oolite (Early Bajocian, "*fissilobatum* hemera" in BUCKMAN 1924), probably from bed 8a of CHANDLER et al. 2006, horizon Bj-5 in CALLOMON 1995, Ovale Zone, based on newly collected topotypes), Bj 6b, however, cannot be excluded with certainty.

Studied material: 10 specimens.

Stratigraphic range: Ovale Zone.

Records: England, Spain, Portugal, Southern Alps.

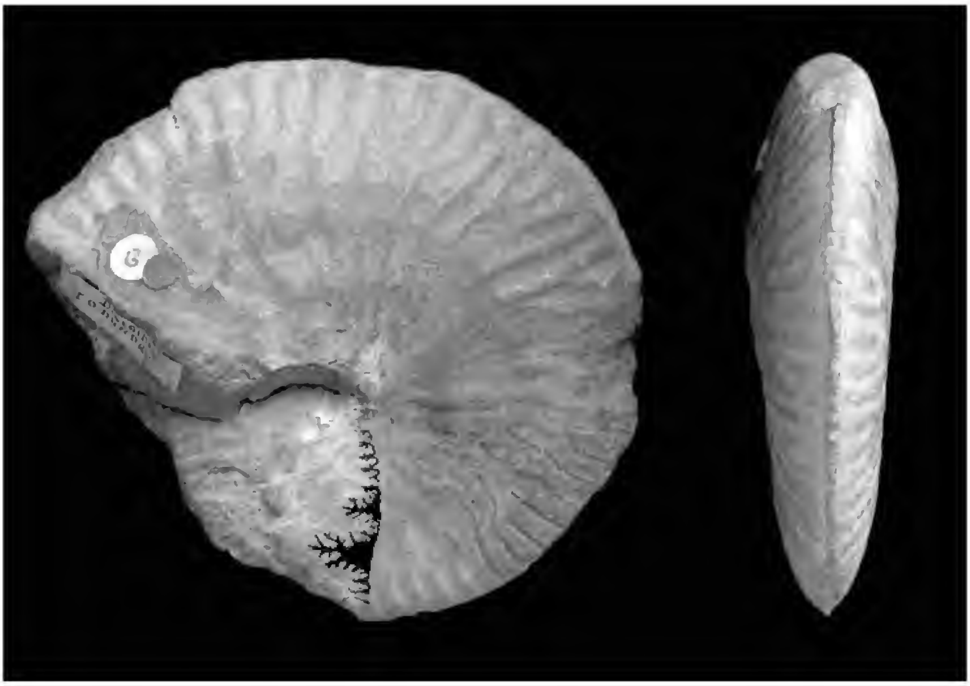


Fig. 5. *Strigoceras compressum* Buckman, neotype, lateral and ventral views (= specimen figured by Buckman 1924, pl. 468); Dundry, West End, Castle Farm; Inferior Oolite, Lower Bajocian, "*fissilobatum* hemera" (= Ovale Zone, horizon Bj-5 or Bj-6b of Callomon 1995, reconstructed after topotypes); BNHM C.41727 (J. W. Tutcher collection). – ×1.

Diagnosis. – *Strigoceras* with slender cross sections, weakly developed lateral furrow, radiate to rectiradiate polyschizotome ribbing which is extremely coarse.

Description. – The neotype of *Strigoceras compressum* is an internal mould with some poor remnants of the shell preserved. Two thirds of the outer whorl is body-chamber. The cross section is oxycone with a partly preserved rounded septicarinate keel. The umbilicus is very narrow. Primary ribs start on the inner third of the flanks and give rise to extremely coarse, very broad, marginally truncated secondaries, with many intercalatory ribs. The ribbing style is polyschizotome. A weak lateral furrow is developed and is visible on the mould. The suture line is extremely complicated consistent with that in other species of *Strigoceras*.

Remarks. – An extremely coarse ribbing is diagnostic for this chronospecies, however, it also occurs in the inner whorls of younger chronospecies, notably in *Strigoceras symplectum* (Buckman, 1924) from the Bajocian, Niortense Zone.

Measurements

	d	h	w	u	r/2	h/d	w/d	u/d
BNHM C.41727SM	~83	49.0	17.5	~3	30	0.59	0.21	0.03
SM X.29140 (Fig. 6)	103.5	57.0	23.2	7.5	(–)	0.55	0.22	0.07

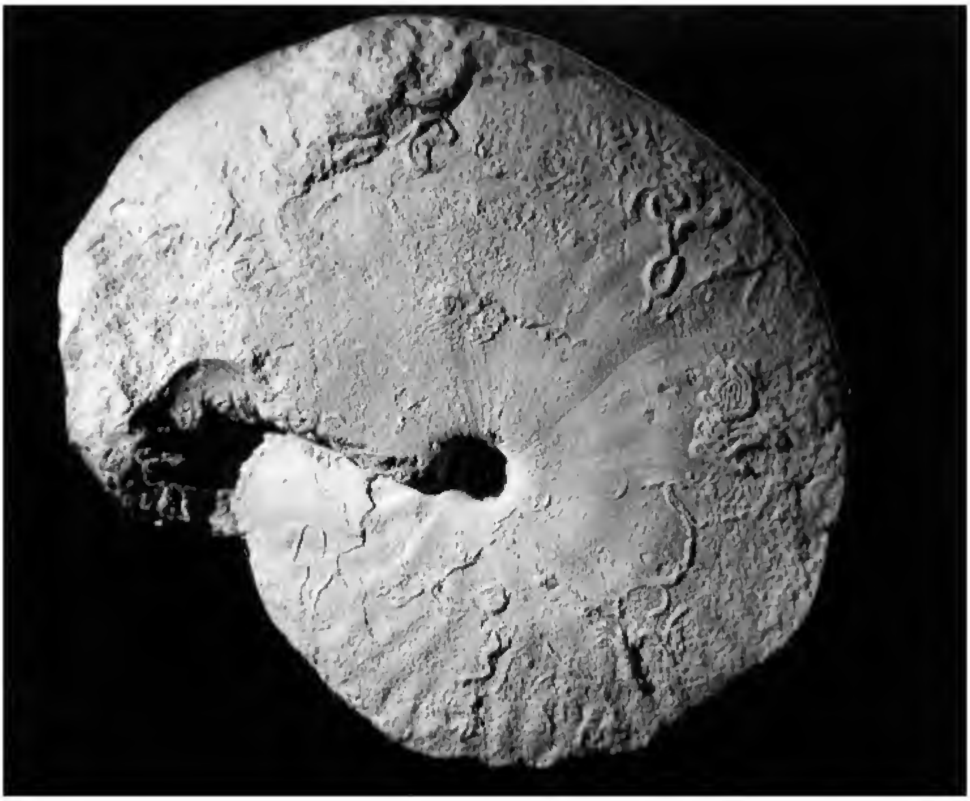


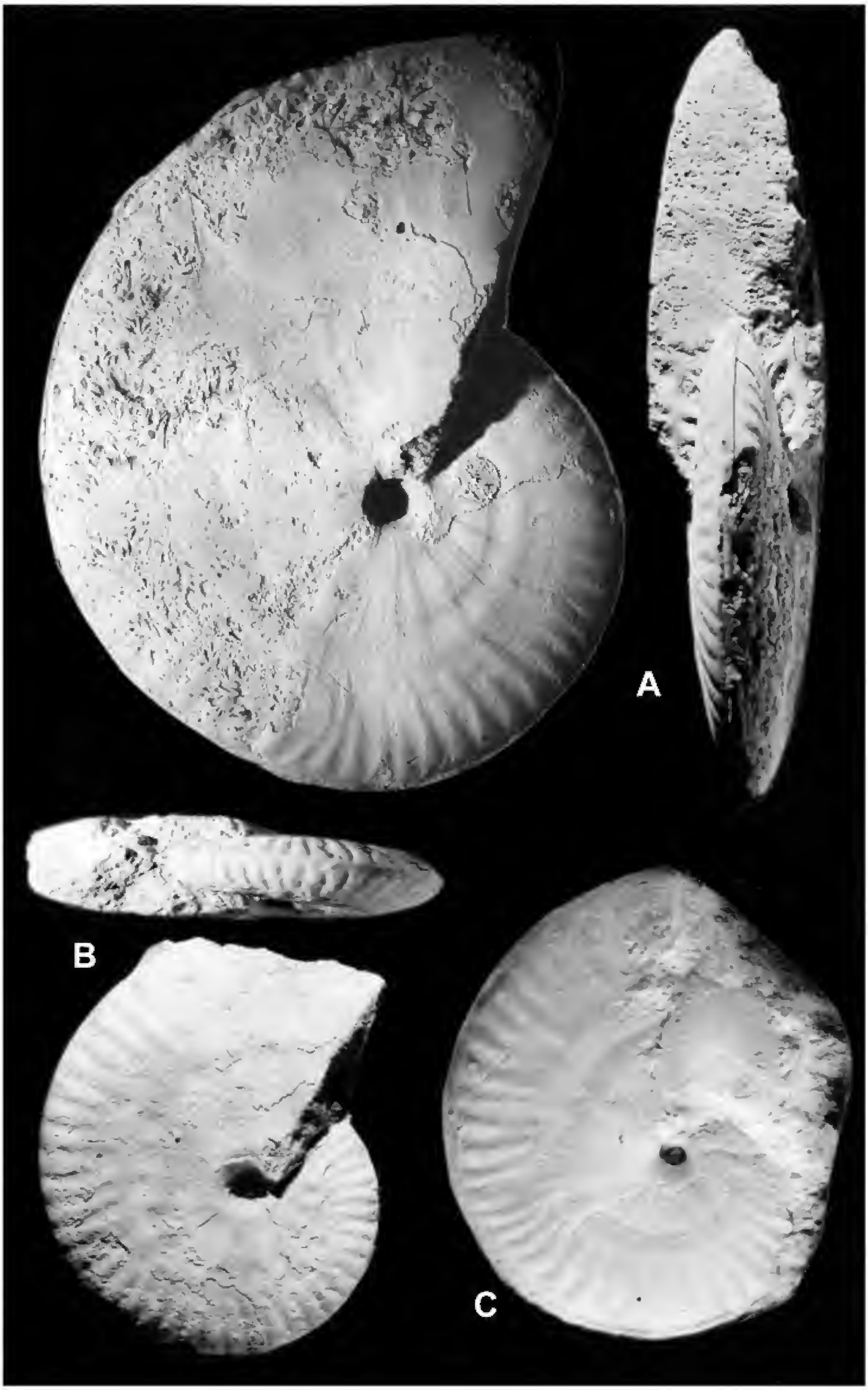
Fig. 6. *Strigoceras compressum* Buckman, lateral view; Dundry, South Main Road Quarry; Inferior Oolite, bed 8a, Lower Bajocian, Ovale Zone, *Witchellia romanoides* horizon (= horizon Bj-5 of Callomon 1995); SM X.29140 (leg. J. H. Callomon, ex RBC collection). – ×1.

Strigoceras strigifer (Buckman, 1924)

Fig. 7A–B

v * 1924 *Strigites strigifer*, nov. – Buckman, pl. 469A (holotype)–B.
v 1955 *Strigoceras pseudostrigifer* n. sp. – Maubeuge, p. 31 pars.
1964 *Strigoceras* cf. *S. languidus* (Buckman). – Imlay, p. 37, pl. 23, figs. 2–4, 8.
1964 *Strigoceras* sp. juv. – Imlay, pl. 23, figs. 5–7.
1965 *Strigoceras strigifer* (Buckman). – Mensink, p. 81.
1967 *Strigites strigifer* Buckman. – Maubeuge, pp. 92–94, text-figs. on pp. 92–93.
1974 *Strigites strigifer* Buckman, 1924. – Atrops, p. 86, pl. 2, fig. 5.
1976 *Strigoceras languidum*. – Morton, p. 27.

Fig. 7. A. *Strigoceras strigifer* (Buckman), holotype, lateral and ventral views; Clatcombe near Sherborne, Dorset; Inferior Oolite, Lower Bajocian, Laeviuscula Zone; BGS GSM 37316. **B.** *Strigoceras strigifer* (Buckman), lateral and ventral views; Oborne, Dorset, Frogden Quarry; Inferior Oolite, Green-Grained Marl, Lower Bajocian, Laeviuscula Zone, Laeviuscula Subzone, *Witchellia laeviuscula* horizon (= horizon Bj-10 of Callomon 1995); SMNS 65360 (leg. G. Dietl). **C.** *Strigoceras languidum* (Buckman), lateral view; Albstadt-Streichen, SW Germany; Ostreenkalk Formation, basal Humphriesioolith Member, Lower Bajocian, Sauzei Zone; SMNS 65364 (leg. G. Stappenbeck). – ×1.


A
B
C

1979 *Strigoceras (S.)* sp. – Parsons, p. 138.
1979 *Strigoceras* sp. – Fernández López & Suárez-Vega, p. 6.
1983 *Strigoceras strigifer.* – Sandoval, p. 117, text-fig. 54, tab.-pl. 77a.
1983 *Strigoceras* sp. – Sandoval, p. 117, text-fig. 54, tab.-pl. 77a.
1985 *Strigoceras strigifer* (Buckman) 1924. – Fernández López, p. 133, pl. 12, fig. 7.
1988 *Strigoceras.* – Galácz, p. 220.
v 1990 *Strigoceras strigifer.* – Calloman & Chandler, p. 98.
1990 *Strigoceras strigifer.* – Cresta & Galácz, p. 168.
1991 *Strigoceras strigifer* Buckman. – Cecca et al., p. 92.
? 1994 *Strigoceras.* – Sadki, tab.-fig. 3. – [1994a].
1996 *Strigoceras languidum* (Buck). – Sadki, p. 139, text-figs. 13, 46.
1997 *Strigoceras strigifer.* – Rioult et al., p. 47.
1998 *Strigoceras strigifer.* – Pavia & Martire, p. 168.

Holotype: Buckman 1924, pl. 469A, BGS GSM 37316, re-figured here as Fig. 7A.
Paratype: Buckman 1924, pl. 469B, BGS GSM 37317.
Type locality: Clatcombe near Sherborne, Dorset.
Type horizon: Inferior Oolite (Early Bajocian, Laeviuscula Zone, as indicated by Buckman 1924). The paratype is said to come from the *Astarte spissa* Bed = Green-grained Marl of Dorset, the age of which is late Laeviuscula Zone.
Studied material: 10 specimens.
Stratigraphic range: Laeviuscula Zone.
Records: England, France, Spain, Portugal, Switzerland, Southern Alps, Apennines, Algeria, Morocco, Alaska (Peninsular Terrane).

Diagnosis. – *Strigoceras* with slender cross section, weakly developed lateral furrow, rectiradiate to rursiradiate, moderately coarse polyschizotome ribbing.

Description. – The holotype of *Strigoceras strigifer* is a moderately large internal mould with remains of the striate shell and the rounded keel in the first half of the last whorl that is still completely septate. The cross section is oxyconic with a very narrow umbilicus that is a little larger in the adult stage. The ornament consists of weak radiate primary ribs starting on the inner third of the flanks giving rise to coarse, very broad, marginally truncated secondaries. The ribbing style is more or less falcoid – slightly polyschizotome. On the flanks, a lateral furrow is developed but interrupted by the primaries.

Remarks. – The paratype of *Strigoceras strigifer* was separated from *Strigoceras* by Maubeuge (1955) and interpreted as belonging to his newly erected species *Strigites pseudostrigifer*. The paratype of *S. strigifer* is nearly from the same horizon as the holotype and doubtlessly belongs to the same chronospecies. Slight differences in sculpture between the two specimens result from differences in the onset of the adult stage and do not justify placing in different taxa. The holotype of *S. pseudostrigifer* is a juvenile specimen from the Humphriesianum Zone of Switzerland (see below).

Measurements

	d	h	w	u	r/2	h/d	w/d	u/d
GSM 37316 (holotype)	112.0	66.0	25.0	5.5	–	0.59	0.22	0.05
dito	74.0	40.5	17.0	4.5	25	0.55	0.23	0.06

Strigoceras languidum (Buckman, 1924)
Figs. 7C, 8–9

v 1893 *Strigoceras* sp. – Buckman, p. 494.
1911 *Oppelia (Strigoceras) Truellei* d'Orbigny sp. – Flamand, p. 884, pl. 4, fig. 14.
v * 1924 *Leptostrigites languidus*, nov. – Buckman, pl. 477A–B.
? 1940 *Strigoceras Truellei* d'Orb., sp. – Verlet & Roch, p. 82.
1955 *Strigoceras strigifer* (Bu.). – Westermann, pp. 519ff.
v ? 1958 *Strigoceras septicarinatum* (Buckman, 1924). – Westermann, p. 54, pl. 17, fig. 6.
1968 *Strigoceras* cf. *strigifer*. – Pavia & Sturani, p. 311.
1972 *Strigoceras* sp. cf. *S. languidum* (Buckman). – Sato, p. 285, pl. 34, figs. 12–13.
1974 *Strigoceras strigifer* (S. B.). – Parsons, p. 166.
v 1975 *Strigoceras strigifer* (Buckman). – Hinkelbein, p. 149, tab.-figs. 11–12, 14.
v 1975 *Strigoceras pseudostrigifer* (Maubeuge). – Hinkelbein, p. 149, tab.-figs. 11–14.
1975 *Strigoceras bessinum* Brasil. – Morton, p. 86, pl. 16, figs. 3–4.
1976 *Strigoceras? languidum* (Buckman). – Morton, p. 27.
1977 *Strigoceras strigifer* (Buckman). – Fernández López, p. 50.
1979 *Leptostrigites languidus*. – Parsons, p. 148, table 4.
1983 *Strigoceras strigifer* (Buck.). – Sandoval, p. 118, text-figs. 60, 77A.
1985 *Strigoceras langidum* (Buckman) 1924. – Fernández López, p. 135, pl. 13, figs. 1–2 [small adults].
1985 *S. (Strigoceras) pseudostrigifer* (Maubeuge, 1955). – Sandoval, p. 94, pl. 1, figs. 4–7.
1986 *Strigoceras* sp. – Sadki et al., p. 455.
1986 *Strigoceras* cf. *languidus* Buck. – Sadki et al., p. 455.
1988 *Strigoceras* cf. *languidum* (Buckman, 1924). – Seyed-Emami, p. 76, text-fig. 23.
1988 *Strigoceras languidum*. – Fernández López et al., tab.-fig. 2.
1988 *Strigoceras languidum* (Buck.). – Fernández López et al., p. 55.
1988 *Strigoceras* cf. *languidum* (Buck.). – Fernández López et al., p. 177.
1988 *Strigoceras pseudostrigifer* (Maubeuge). – Fernández López et al., p. 177.
1988 *Strigoceras* cf. *languidum*. – Fernández López & Aurell, tab.-fig. 4.
1990 *Strigoceras pseudostrigifer*. – Sandoval, pp. 147, 149.
1990 *Strigoceras longuidum*. – Seyed-Emami & Alavi-Naini, tab.-pl. 2.
1991 *Strigoceras strigifer*. – Galácz, p. 111.
1992 *Strigoceras* cf. *longuidum*. – Sato in Westermann, p. 205.
? 1994 *Strigoceras*. – Sadki, tab.-fig. 4. – [1994a].
? 1994 *Strigoceras strigifer*. – Sadki, tab.-fig. 4. – [1994a].
v 1995 *Strigoceras* cf. *pseudostrigifer* (Maubeuge). – Ohmert et al., p. 69.
1996 *Strigoceras strigifer* (Buck). – Sadki, tab.-figs. 14, 46.
1996 *Strigoceras* sp. – Sadki, p. 73.
1996 *Strigoceras pseudostrigifer* (Maub.). – Sadki, p. 142, tab.-fig. 46.
1997 *Strigoceras* sp. – Rioult et al., p. 47.
1998 *Strigoceras longuidum*. – Seyed-Emami et al., pl. 2.
v 2000 *Strigoceras languidum*. – Huxtable, p. 104.
v 2001 *Strigoceras* sp. – Chandler & Dietze, p. 115, text-fig. 2.
2002 *Strigoceras* sp. – Cresta et al. in Santantonio, p. 231.
v 2006 *Strigoceras langidum* (Buckman). – Chandler et al., text-fig. 2.

Holotype: Buckman 1924, pl. 477A, BGS GSM 37324, re-figured here as Fig. 8B.

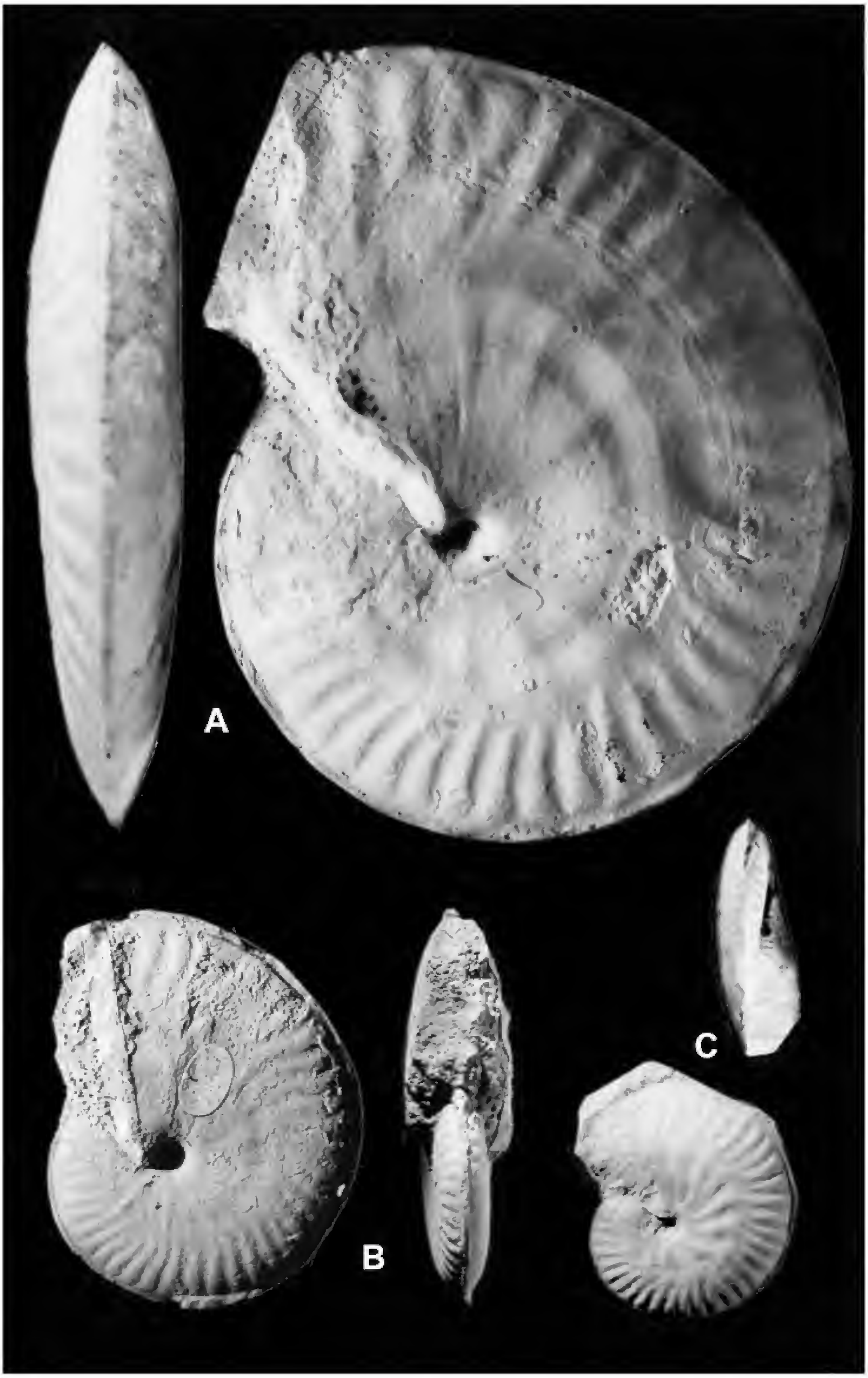
Paratype: Buckman 1924, pl. 477B, BGS GSM 37325.

Type locality: Sandford Lane, Dorset, England.

Type horizon: Inferior Oolite, Fossil Bed, upper part (bed 6b of Buckman 1893), Sauzei Zone, horizon Bj-11 in Callomon (1995). The paratype comes from the Inferior Oolite, bed 10a of South Main Road Quarry (Bajocian, Sauzei Zone) at Dundry Hill near Bristol, see Parsons (1979: 148) and Chandler et al. 2006: fig. 1).

Stratigraphic range: Sauzei Zone.

Studied material: ca. 30 specimens.


A
B
C

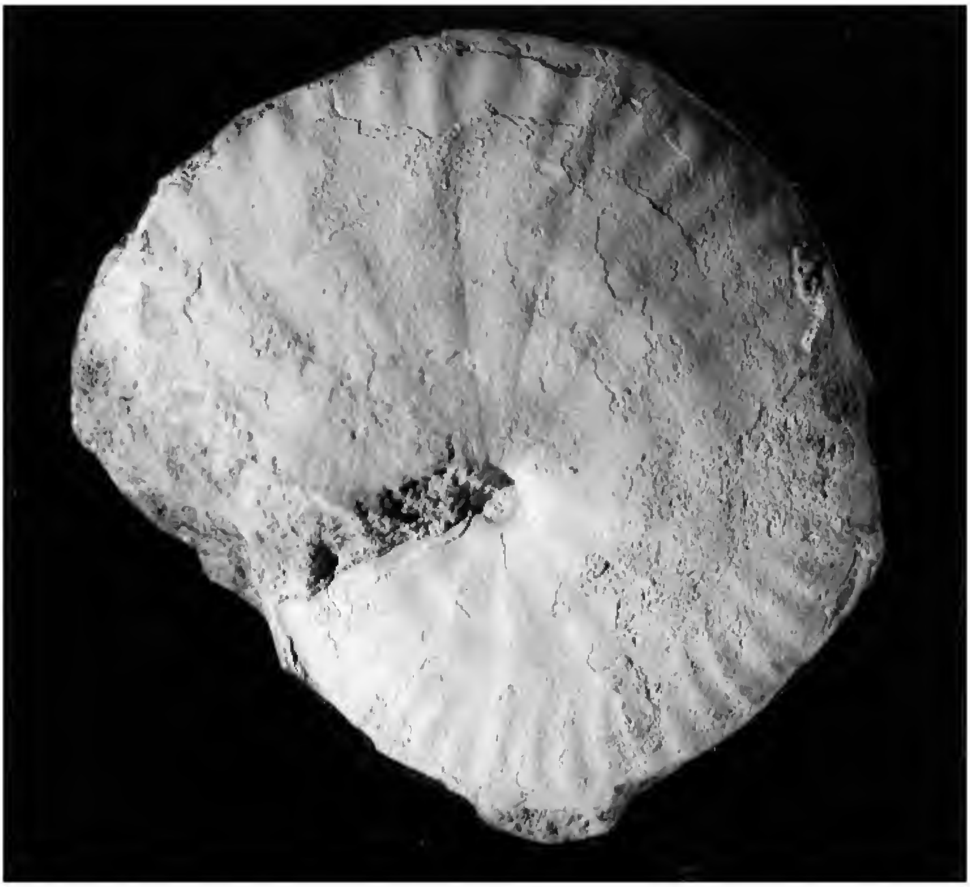


Fig. 9. *Strigoceras languidum* (BUCKMAN), lateral view; Oborne, Frogden Quarry; Inferior Oolite, bed 4a (section see CALLOMON 1995), Lower Bajocian, Sauzei Zone (horizon Bj-11 of CALLOMON 1995); SM X40232 (leg. R. B. CHANDLER). – ×1.

Records: England, Scotland, France, SW Germany (this study, Fig. 7C), ? NW Germany, Spain, Apennines, Hungary, Algeria, Morocco, Iran, Japan.

Diagnosis. – *Strigoceras* with slender cross section, weakly developed lateral furrow, rectiradiate to rursiradiate, polyschizotome ribbing.

Description. – The holotype of *S. languidum* is small and has a slender, oxyconic whorl section. Falcoid ribbing persists up to the last preserved whorl display-

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Fig. 8. *Strigoceras languidum* (BUCKMAN), lateral and ventral views. **A.** Topotype; Sandford Lane near Sherborne, Dorset; Inferior Oolite, bed 6b, Lower Bajocian, Sauzei Zone (horizon Bj-11 of CALLOMON 1995); SMNS 67153 (ex coll. V. DIETZE). **B.** Holotype; Sandford Lane near Sherborne, Dorset; Inferior Oolite, Lower Bajocian, Fossil Bed, upper part, Sauzei Zone (horizon Bj-11 of CALLOMON 1995); BGS GSM 37324. **C.** Juvenile specimen; Riodeva, Keltiberian Ranges, E Spain; Chelva Formation, bed 7 in section F of HINKELBEIN (1975, text-fig. 13), Lower Bajocian, Sauzei Zone; SMNS 65362 (Coll. K. HINKELBEIN). – ×1.

ing regularly arranged retrocostate secondaries. The umbilicus is very narrow. Lateral furrows are not seen due to the internal mould preservation.

Comparisons. – *S. languidum* differs mainly from older chronospecies e.g. *S. strigifer* (Buckman) in its overall denser and finer ribbing, in which primaries are barely visible and the medium longitudinal furrow is interrupted by ribs crossing it.

Measurements

	d	h	w	u	r/2	h/d	w/d	u/d
GSM 37324 (holotype)	57.0	31.5	15.0	4.0	~21	0.55	0.26	0.07
RBC 28	43.0	25.0	9.5	2.8	28	0.58	0.22	0.07
RBC 19	68.0	40.0	15.3	4.5	27	0.59	0.23	0.07
SM X40232 (Fig. 9)	~98	~57	24.0	4.0	25	0.58	0.24	0.04
SMNS 67153 (Fig. 8A)	116.3	68.5	28.0	4.5	22	0.59	0.24	0.04

Strigoceras bessinum Brasil, 1895

Figs. 10–12

v 1857 *Ammonites Truellei.* – Quenstedt, p. 395, pl. 54, fig. 6.
pars 1878 *Amaltheus Truellei.* – Neumayr, p. 68.
v 1886 *Ammonites Truellei gracilis.* – Quenstedt, p. 568, pl. 69, fig. 10 (= holotype of *S. gracile*, see Hölder 1964: 98).
* 1895 *Strigoceras bessinum* nov. sp. – Brasil, p. 43, pl. 4, figs. 6–7.
? 1924 *Strigoceras Truellei.* – Wetzel, p. 210.
1952 *Strigoceras* sp. – Kumm, p. 388.
? 1952 *Strigoceras truellei.* – Kumm, p. 413.
1953 *Strigoceras* sp. – Mouterde, pp. 91 f., 123.
1954 *Strigoceras symplectum.* – Westermann, p. 25.
1955 *Strigites pseudostrigifer* n. sp. – Maubeuge, p. 31 pars, pl. 11, fig. 5, pl. 2, fig. 8, pl. 5, fig. 3.
1964 *Strigoceras* aff. *strigifer* (S. Buckm.). – Sturani, p. 26, pl. 4, fig. 6. – [1964b].
1964 *Strigoceras* cf. *S. languidum.* – Imlay, pl. 23, figs. 2–4, 8.
1971 *Strigoceras bessinum* Brasil. – Sturani, pl. 4, figs. 17–19.
1971 *Strigoceras* sp. ind. juv. aff. *strigifer* (S. Buckman). – Sturani, p. 119, pl. 4, figs. 11–15.
1971 *Strigoceras* sp. ind. juv. cf. *strigifer* (S. Buckm.) – Sturani, p. 119, pl. 16, fig. 10.
1971 *Strigoceras strigifer.* – Whicher & Palmer, p. 117.
v 1975 *Strigoceras symplectum* (Buckman). – Hinkelbein, tab.-fig. 12.
? 1976 *Strigoceras* cf. *compressum.* – Morton, p. 28.
? 1976 *Strigoceras (S.) bessinum* Brasil. – Parsons, p. 131.
1978 *Stringoceras* sp. – Sequeiros et al., p. 296.
1979 *Strigoceras* aff. *strigifer.* – Linares & Sandoval, tab.-fig. 2.
v 1980 *Strigoceras.* – Dietl & Rieber, pp. 61, 65.
1983 *Strigoceras* sp. – Sandoval, p. 120, tab.-fig. 77A pars.
1983 *Strigoceras* aff. *strigifer* Buck. – Sandoval, p. 119–120, tab.-fig. 77A pars.
1985 *S. (Strigoceras) paronai.* – Sandoval, pl. 1, fig. 10.
1985 *S. (Strigoceras) truellei.* – Sandoval, pl. 2, fig. 3.
1985 *Strigoceras* cf. *strigifer* (Buckm.). – Schatz, fig. 5.
1988 *Strigoceras bessinum* Brasil. – Fernández Lopéz, p. 76.
1988 *Strigoceras paronai* (Trauth). – Fernández Lopéz et al., p. 178. – [1988a].
v 1990 *Strigoceras* sp. – Ohmert, text-fig. 2.
v 1990 *Strigoceras.* – Gassmann & Ohmert, p. 164.
1990 *Strigoceras strigifer.* – Sandoval, tab.-fig. 6.
1992 *Strigoceras* cf. *languidum.* – Poulton et al. in Westermann, p. 72.
1994 *Strigoceras* sp. – Fernández Lopéz & Mouterde, p. 122 pars. – [1994a].
v 1995 *Strigoceras pseudostrigifer* (Maubeuge). – Ohmert et al., p. 67, pl. 4, figs. 6–8.

v 1995 *Strigoceras egertense* n. sp. – Ohmert et al., p. 69, pl. 4, figs. 9–10.
v 1995 *Strigoceras bessinum* Brasil. – Ohmert et al., p. 72, pl. 4, fig. 4.
1996 *Strigoceras* sp. – Sadki, tab.-fig. 46 pars.
? 1997 *Strigoceras bessinum*. – Rioult et al., p. 47.
1997 *Strigites pseudostrigifer*. – Rulleau, pl. 5, figs. 1–2.
1997 *Strigites strigifer*. – Rulleau, pl. 5, figs. 4–5.
2000 *Strigoceras* sp. – Huxtable, p. 105.
2004 *Strigoceras* cf. *strigifer* (Buckman). – Krobicki & Wierzbowski, pp. 73, 75.
2006 *Strigoceras strigifer* Buckman. – Rulleau, p. 112, pl. 88, fig. 1.
2006 *Strigoceras pseudostrigifer* Maubeuge. – Rulleau, p. 112, pl. 88, fig. 2.

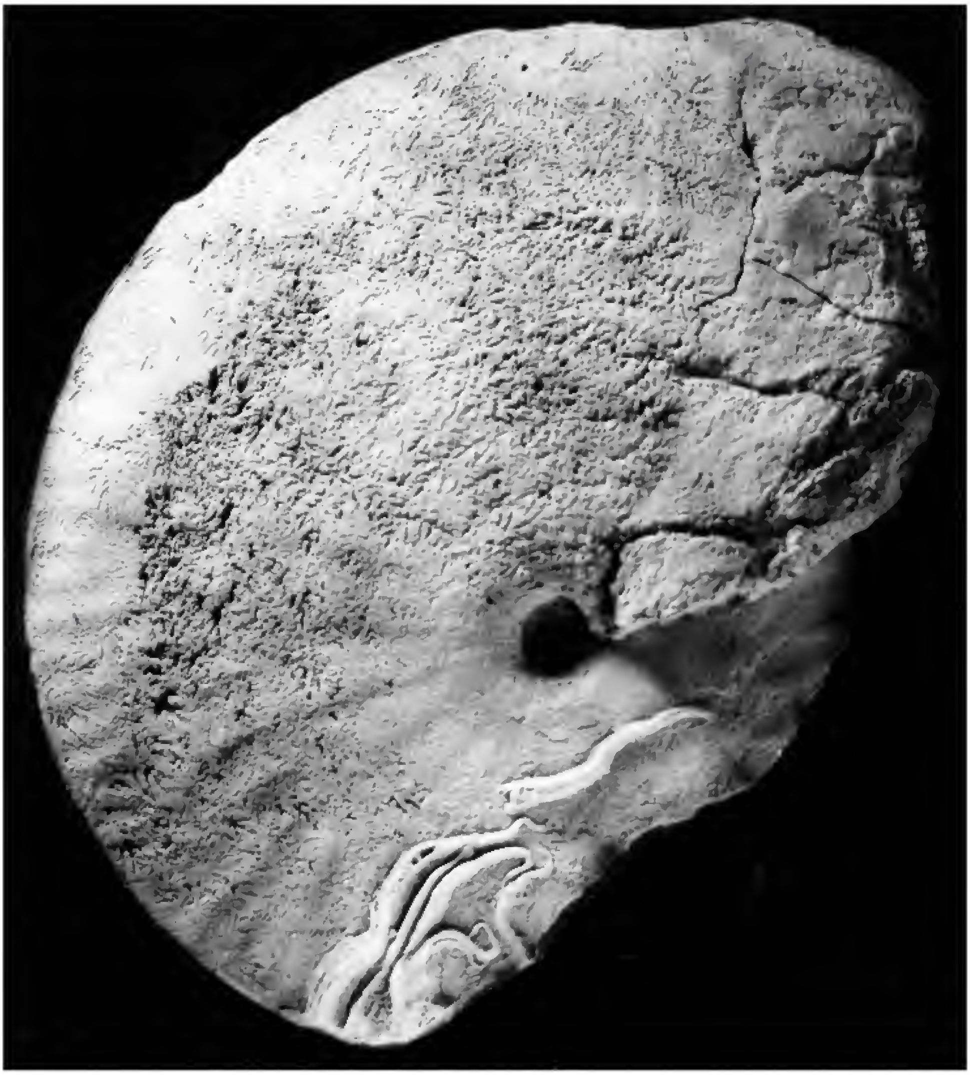
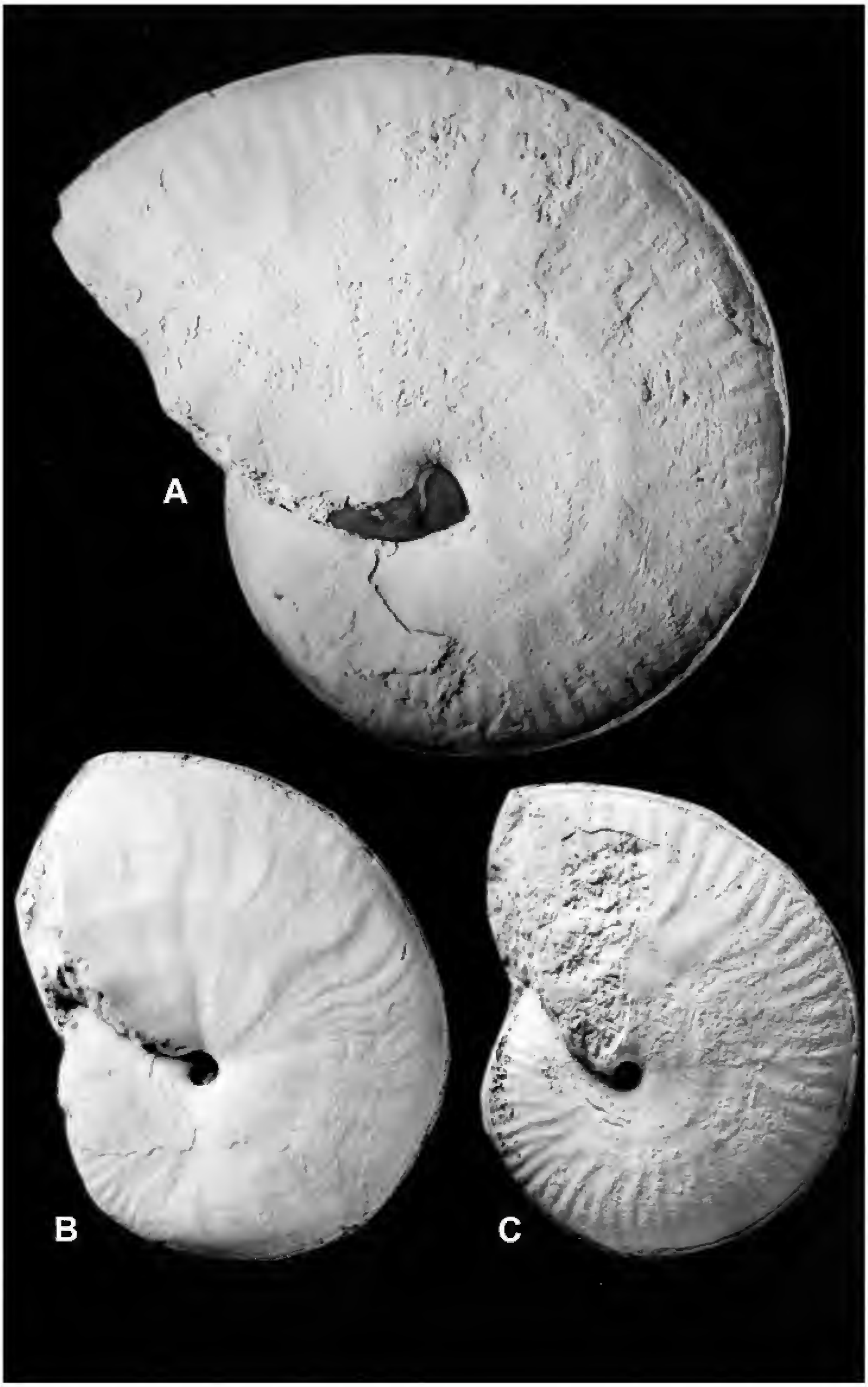


Fig. 10. *Strigoceras bessinum* Brasil var. *symplectum* (Buckman) (= holotype of *Ammonites truellei gracilis* Quenstedt 1986, pl. 69, fig. 10), lateral view; Spaichingen, SW Germany; Lower Bajocian, Humphriesioolith Formation, Humphriesianum Zone, probably *Poecilomorphus cycloides* horizon (after lithology of the matrix); IFGT, Quenstedt collection, without number. – ×1.


A
B
C

Taxonomic remarks. – The specific name *Ammonites truellei gracilis* Quenstedt, 1886 is not valid because it is preoccupied by the older homonym *Ammonites gracilis* Zieten, 1830 (for the treatment of Quenstedt's trinomina see Callomon et al. 2004a, b; International Commission on Zoological Nomenclature 2005). We replace this name by its next younger subjective synonym introduced by Brasil (1895). *Strigites pseudostrigifer* Maubeuge, 1955 is based on a juvenile specimen from the Humphriesianum Zone of Switzerland and represents a coarser ribbed variety of the chronospecies *Strigoceras bessinum* Brasil, 1895.

Holotype: Brasil (1895, pl. 4, figs. 6–7), depository unknown, probably housed in the collections of the University of Caen, France.

Type locality: Vicinity of Bayeux, Normandy, France.

Type horizon: Oolithe ferrugineuse de Bayeux (Late Bajocian, Humphriesianum Zone, probably Romani Subzone, horizon à *Dorsetensia edouardiana*).

Stratigraphic range: Humphriesianum Zone.

Studied material: Ca. 25 specimens.

Records: England, France, Spain, Morocco, SW Germany, Switzerland, Southern Alps, Sicily, Polish Carpathians.

Diagnosis. – *Strigoceras* with slender cross section, one weakly developed lateral furrow; weak rectiradiate, polyschizotome ribbing.

Description. – See Brasil (1895). The holotype of *Strigoceras bessinum* from the Humphriesianum Zone is a dwarf variant of this chronospecies, becoming almost smooth very early in ontogeny (see p. 44). Although the typical '*bessinum*' morphology seems to be restricted to the Humphriesianum Zone, where it is rather abundant, the average morphology is represented by much larger and stronger ribbed specimens figured here (see also Rulleau 2006, figs. 1–2). These differ from the older chronospecies *S. languidum* (Buckman) in a denser and more radiate ribbing at a medium growth stage. In the younger chronospecies *S. symplectum* (Buckman) the lateral furrow is more accentuated, and the width of the cross section is larger. Morphologically transitional specimens are common. Taxonomically, they can be treated as variety *symplectum* (Buckman) within the chronospecies *S. bessinum* (Brasil) (e. g. Figs. 10, 11A, 12).

Measurements

	d	h	w	u	r/2	h/d	w/d	u/d
Holotype (after Brasil 1895)	26.0	14.0	6.0	2.0	–	0.54	0.23	0.07
SMNS 65367 (Fig. 11C)	71.0	42.0	~14	3.7	30	0.59	0.20	0.05
SM X40233 (Fig. 11B)	75.7	43.0	(–)	5.2	–	0.57	–	0.07
SMNS 65368 (Fig. 12)	~104	61.7	~22	4.3	31	0.59	0.21	0.04

Fig. 11. A. *Strigoceras bessinum* Brasil var. *symplectum* (Buckman), lateral view; Oborne, Frogden Quarry, Inferior Oolite, bed 4b (section see Callomon 1995), Lower Bajocian, Humphriesianum Zone, Romani Subzone (horizon Bj-14b of Callomon 1995); SMNS 67154 (ex coll. V. Dietze). **B.** *Strigoceras bessinum* Brasil, lateral view; same locality and bed as Fig. 11A; SM X40233 (ex RBC collection). **C.** *Strigoceras bessinum* Brasil var. *symplectum* (Buckman), lateral view; Thurnau, Kanton Baselland, Switzerland; Humphriesioolith Formation, Lower Bajocian, Humphriesianum Zone, Humphriesianum Subzone; SMNS 65367. – ×1.

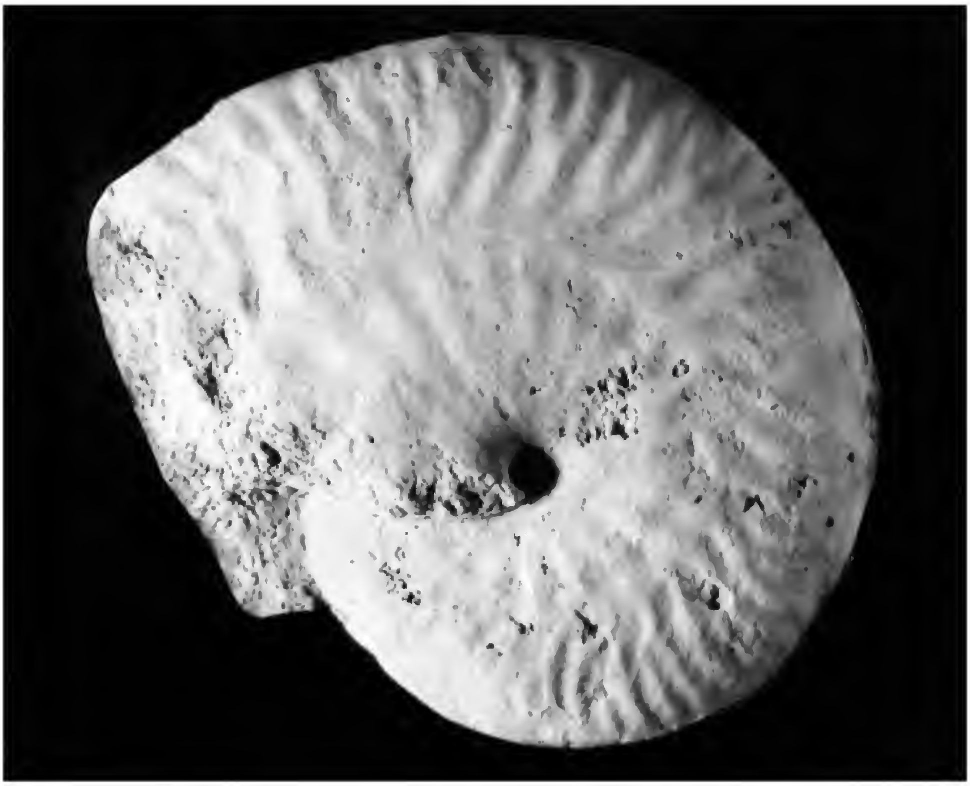


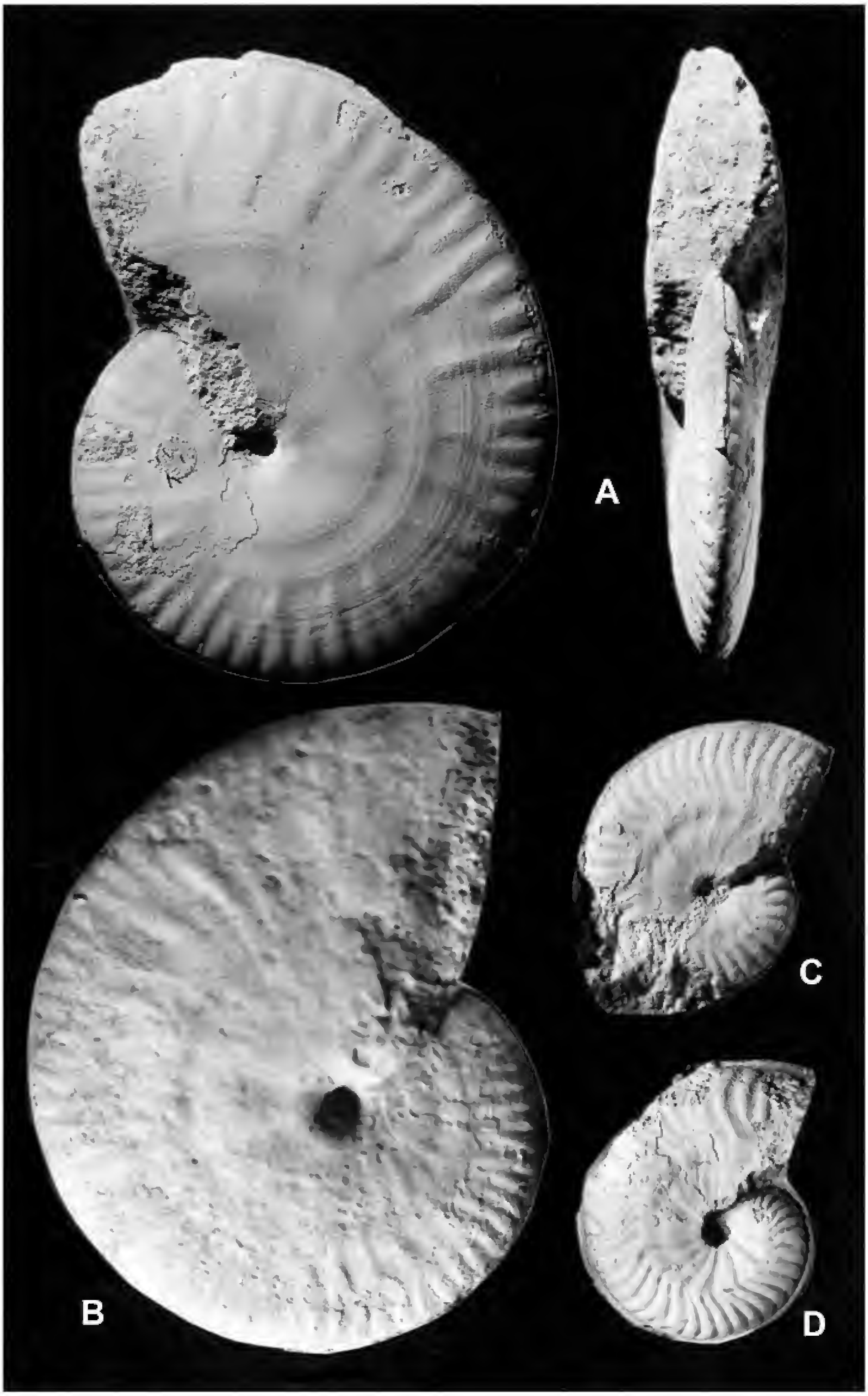
Fig. 12. *Strigoceras bessinum* Brasil var. *symplectum* (Buckman), lateral view; Öfingen, SW Germany; Humphriesioolith Formation, Lower Bajocian, Humphriesianum Zone, Humphriesianum Subzone, probably *Stephanoceras umbilicum* horizon; SMNS 65368 (ex coll. N. Wannenmacher). – × 1.

Strigoceras symplectum (Buckman, 1924)

Figs. 13–15, 16A–F

v pars 1886 *Ammonites Truellei trifurcatus.* – Quenstedt, p. 567, pl. 69, fig. 9, non fig. 8.
v ? 1886 *Ammonites Truellei.* – Quenstedt, p. 570, pl. 69, fig. 13.
1891 *Ammonites Truellei.* – Haug, p. 74.
v 1893 *Strigoceras.* – Buckman, p. 500.
1896 *Hecticoceras* (?) *pingue* Par. – Parona, p. 12, pl. 1, fig. 5.
1896 *Lunuloceras canovincola* de Greg. – Parona, p. 13, pl. 1, fig. 6.
1896 *Oppelia? propefusca* de Greg. – Parona, p. 14, pl. 1, figs. 8–9.
1906 *Strigoceras Truellei* d'Orb. – Lissajous, p. 693.
1923 *Oppelia paronai.* – Trauth, pp. 183, 185. – [1923a].
? 1923 *Strigoceras Truellei* d'Orb. sp. – Fallot & Blanchet, pl. 4, fig. 8; pl. 6, fig. 5; pl. 9, fig. 4.
v * 1924 *Plectostrigites symplectus*, nov. – Buckman, pl. 471.
v pars 1928 *Strigoceras Parkinsoni* Qu. – Scheurlen, pl. 1, fig. 12, non figs. 13–16 [= *Phlycticeras dorsocavatum* (Quenstedt), see Schweigert & Dietze 1998].
1939 *Strigoceras* cf. *strigifer* Buckman. – Roché, p. 166, pl. 6, fig. 3.
1958 *Strigoceras* sp. juv. cf. *compressus.* – Wilson et al., p. 96.
pars 1964 *Strigoceras truellei.* – Rioult, p. 245.

1968 *Strigoceras truellei.* – Pavia & Sturani, p. 314.
1970 *Strigoceras truellei* (d'Orb.). – Galácz, p. 118.
1971 *Strigoceras paronai* (Trauth). – Sturani, p. 121, pl. 4, figs. 1 (= lectotype), 2–5, 10.
1971 *Strigoceras truellei* (d'Orb.). – Sturani, p. 120, pl. 4, figs. 6–9.
1971 *Strigoceras* aff. *bessinum* Brasil. – Sturani, p. 118, pl. 4, fig. 16.
1971 *Strigoceras* sp. ind. juv. cf. *septicarinatum* (S. Buckm.). – Sturani, p. 120, pl. 16, fig. 9.
v 1971 *Strigoceras* sp. indet. – Wendt, pp. 157f.
1973 *Strigoceras truellei* (d'Orbigny). – Pavia, pl. 16, fig. 10.
v pars 1974 *Strigoceras truellei* (d'Orb.). – Dietl, table 1.
v pars 1975 *Strigoceras truellei* (d'Orbigny). – Hinkelbein, p. 153, tab.-figs. 11–12, 14.
v pars 1975 *Strigoceras septicarinatum* (Buckman). – Hinkelbein, tab.-figs. 11–12.
1976 *Strigoceras (Strigoceras)* sp. – Parsons, pp.126, 129.
1978 *Strigoceras truellei* (d'Orb.). – Sequeiros et al., p. 297.
v 1979 *Strigoceras symplectum.* – Dietl & Hugger, tab.-fig. 2.
v 1979 *Strigoceras septicarinatum.* – Dietl & Hugger, tab.-fig. 2.
v 1979 *Strigoceras truelli.* – Dietl & Hugger, tab.-fig. 2.
1979 *Strigoceras truelli.* – Linares & Sandoval, text-figs. 2–3.
1980 *Strigoceras truellei* (d'Orbigny). – Galácz, p. 54, pl. 11, fig. 4.
1982 *Strigoceras truellei.* – Fernández López, tab.-fig. 2.
1983 *Strigites pseudostrigifer.* – Pavia, pl. 8, figs. 1–2.
pars 1983 *Strigoceras* aff. *strigifer* Buck. – Sandoval, p. 122, figs. 67, 77A.
pars 1983 *Strigoceras* sp. – Sandoval, p. 122, figs. 67, 77A.
pars 1983 *S. truellei* "sensu" Pavia. – Sandoval, p. 122, figs. 67, 77A.
pars 1983 *S. paronai* (Trauth). – Sandoval, p. 122, figs. 67, 77A.
1984 *Strigoceras strigifer.* – Dietl & Pavia, p. 328.
1984 *Strigoceras pseudostrigifer.* – Dietl & Pavia, pp. 328, 331, tab.-fig. 3.
1985 *Strigoceras truellei* (d'Orbigny) 1845. – Fernández López, p. 127, pl. 12, fig. 6.
1985 *Strigoceras* sp. nov. 1. – Fernández López, p. 137, pl. 13, fig. 3.
1985 *Strigoceras paronai* (Trauth) 1922. – Fernández López, p. 132, pl. 13, fig. 4.
pars 1985 *S. (Strigoceras) truellei* (d'Orbigny, 1845). – Sandoval, p. 98, pl. 2, fig. 4, non fig. 3 [= *S. truellei*].
1986 *Strigoceras (Liroxyites)* cf. *kellumi* Imlay, 1961. – Sandoval & Westermann, p. 123, figs. 12.5–12.6.
1990 *Strigoceras.* – Hegele, p. 317.
1990 *Strigoceras truellei.* – Sandoval, tab.-fig. 7.
1991 *Strigoceras symplectus* (S. S. Buckman). – Huxtable, p. 198.
1992 *Strigoceras (Liroxyites)* cf. *kellumi* Imlay. – Salvador et al., p. 98.
v 1993 *Strigoceras truellei* (d'Orbigny), 1845. – Besnosov & Mitta, p. 23, pl. 1, figs. 4–6.
v 1993 *Strigoceras (Strigoceras) paronai* (Trauth), 1922. – Besnosov & Mitta, p. 24, pl. 1, fig. 7.
1994 *Strigoceras* sp. – Benhamou & Elmi, p. 274.
pars 1994 *Strigoceras* sp. – Fernández Lopéz & Mouterde, p. 122. – [1994a].
1995 *Strigoceras* cf. *truellei.* – Gauthier et al., p. 321.
1995 *Strigoceras truellei* (d'Orb.). – Hegele, p. 222, fig. bottom right and p. 224, fig. bottom right.
1997 *Strigoceras septicarinatum.* – Rioult et al., p. 50.
1997 *Strigoceras pseudostrigifer.* – Rioult et al., p. 50.
1997 *Strigoceras symplectum.* – Rioult et al., p. 50.
1998 *Strigoceras paronai* (Trauth). – Fernández López et al., tab.-fig. 3. – [1998a].
v 2000 *Strigoceras (Strigoceras) truellei* (d'Orbigny). – Besnosov & Mitta, pp. 13, 51, pl. 1, figs. 1–4.
v 2000 *Strigoceras (Strigoceras) paronai* (Trauth). – Besnosov & Mitta, pp. 13, 51, pl. 1, figs. 5–6.
2002 *Strigoceras truellei* (d'Orb.). – Gauthier et al., p. 82.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D

Taxonomic remarks. – The specific name *Ammonites truellei trifurcatus* Quenstedt, 1886 is preoccupied by *Ammonites trifurcatus* Reinecke in Zieten (1830). The next youngest subjective synonym of this chronospecies is *S. paronai* introduced by Trauth (1923a). The lectotype of *S. paronai*, re-figured by Sturani (1971, pl. 4, fig. 1), is a juvenile specimen that does not differ significantly from the nuclei or juveniles of other chronospecies. The ammonites from the *Posidonia alpina* Bed are usually extremely small, immature and dwarfed. Macroconchs predominate due to current sorting in a high-energy environment on a pelagic submarine swell. This is clear because the corresponding microconchs *(Cadomoceras nepos)* exhibit normal diameters in the same bed. Larger specimens of the same age from other localities allow a much better understanding of this species. We take *S. paronai* as a nomen dubium, in favour of *Plectostrigites symplectus* Buckman, 1924.

Holotype: Buckman (1924, pl. 471), BGS GSM 37319, re-figured here as Fig. 13A.
Type locality: Frogden Quarry, Oborne, Dorset, England.
Type horizon: Inferior Oolite, bed 6a (for section see Parsons 1979; Niortense Zone, Baculata Subzone, faunal horizon Bj-23 in Callomon 1995).
Stratigraphic range: Niortense Zone.
Studied material: Ca. 30 specimens.
Records: Spain, France, SW Germany, England, Algeria, Southern Alps, Sicily, Hungary, Caucasus (Dagestan), Turkmenistan, Mexico.

Diagnosis. – *Strigoceras* with a slender cross section, one deep, prominent median lateral furrow, and prorsiradiate polyschizotome ribbing.

Description. – See detailed description in Sandoval (1985: 96) for *Strigoceras paronai* (Trauth). The holotype of *S. symplectum* is a moderately large specimen, partly with shell preserved. It exhibits a prominent longitudinal striation, particular-

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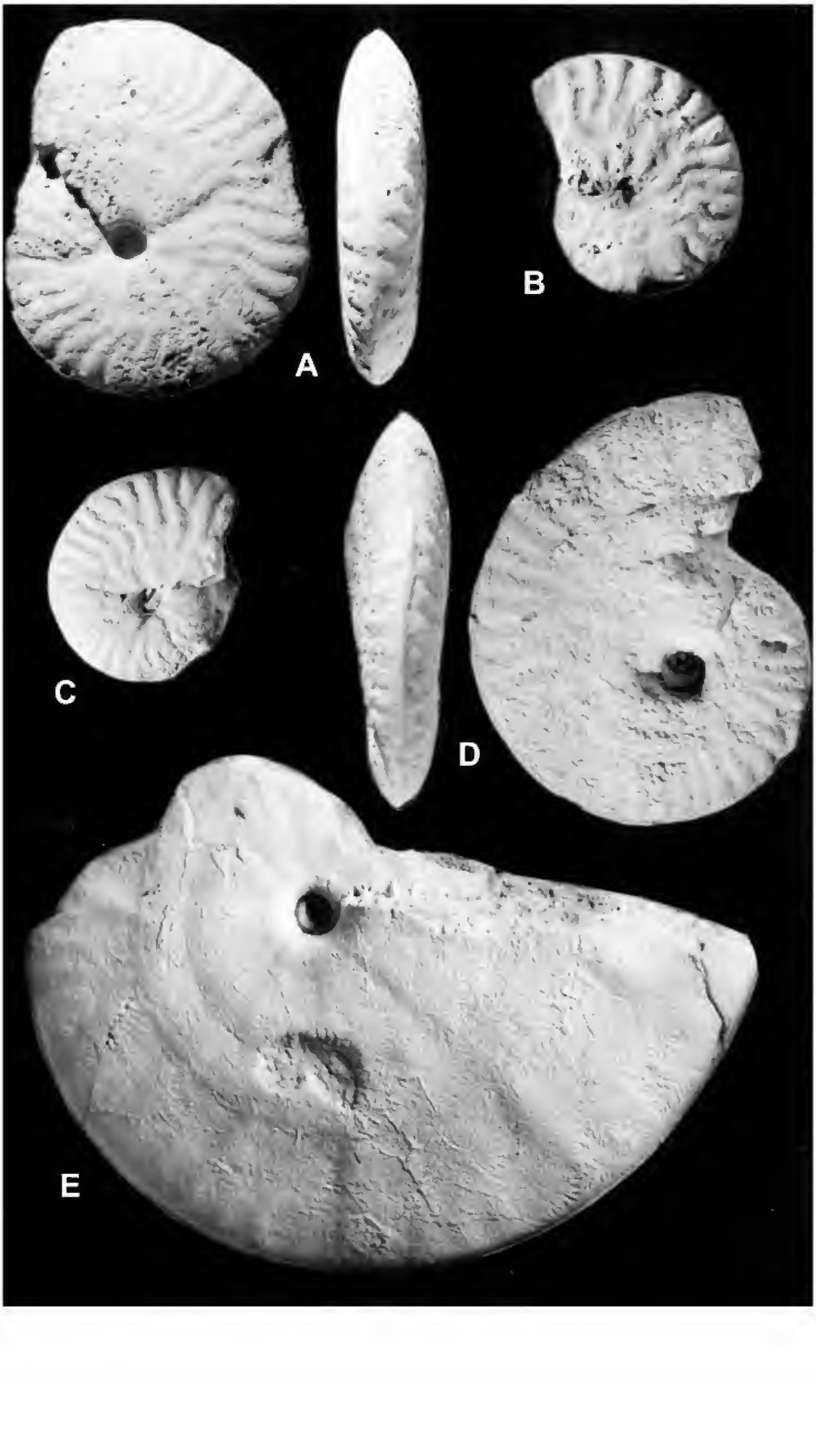
◀ **Fig. 13.** *Strigoceras symplectum* (Buckman). **A.** Holotype, lateral and ventral views; Frogden Quarry, Oborne, Dorset, England; Inferior Oolite, bed 6a (for section see Parsons 1979), Upper Bajocian, Niortense Zone, Baculata Subzone (horizon Bj-23 of Callomon 1995); BGS GSM 37319. **B.** Lateral view; Bretteville-sur-Odon, Normandy, France; Oolithe ferrugineuse de Bayeux, Upper Bajocian, Niortense Zone; SMNS 65377 (Coll. G. Schweigert). **C.** Topotype, lateral view; Oborne, Dorset, Frogden Quarry; Inferior Oolite, bed 6a (for section see Parsons 1979), Upper Bajocian, Niortense Zone, Baculata Subzone (horizon Bj-23 of Callomon 1995); SMNS 65373 (leg. G. Dietl). **D.** Lateral view; Oborne, Dorset, Frogden Quarry; Inferior Oolite, bed 6a (for section see Parsons 1979), Upper Bajocian, Niortense Zone, Banksii Subzone (horizon Bj-20 of Callomon 1995); SMNS 67155 (ex coll. V. Dietze). – ×1.

Fig. 14. *Strigoceras symplectum* (Buckman). **A.** Lateral and ventral views; Streichen near Balingen, SW Germany; Ostreenkalk Formation, Subfurcatenoolith Member, Lower Bajocian, Niortense Zone, Banksii Subzone; SMNS 65371 (leg. G. Dietl & M. Kapitzke). **B.** Lateral view of a juvenile specimen; Zimmern near Balingen, SW Germany; Ostreenkalk Formation, Subfurcatenoolith Member, Upper Bajocian, Niortense Zone; SMNS 65372 (leg. G. Dietl & M. Kapitzke). **C.** Lateral view of a juvenile specimen; Rabanera I, Keltiberian Ranges, NE Spain (for section see Dietl 1974: 6); Chelva Formation, Upper Bajocian, Niortense Zone; SMNS 65374 (leg. G. Dietl). **D.** Ventral and lateral views; Albarracín, Keltiberian Ranges, E Spain; Chelva Formation, bed 27f in section A of Hinkelbein (1975, text-fig. 11), Upper Bajocian, Niortense Zone; SMNS 65375 (Coll. K. Hinkelbein). **E.** Lateral view; motorway cut near Aichelberg, SW Germany; Ostreenkalk Formation, Subfurcatenoolith Member, Upper Bajocian, Niortense Zone, Polygyralis Subzone; SMNS 67156 (ex coll. V. Dietze). – B ×1.5, others ×1. ▶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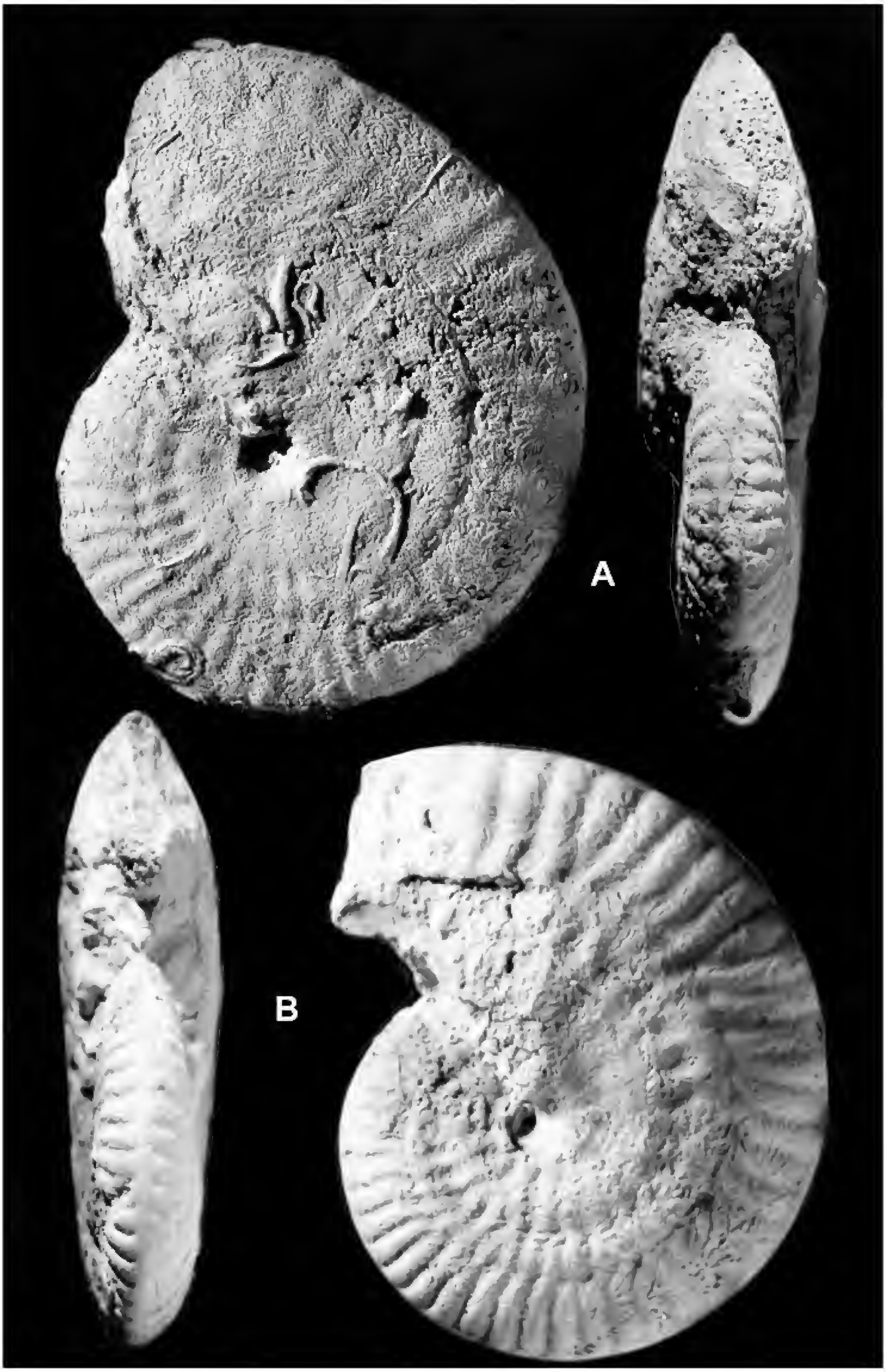
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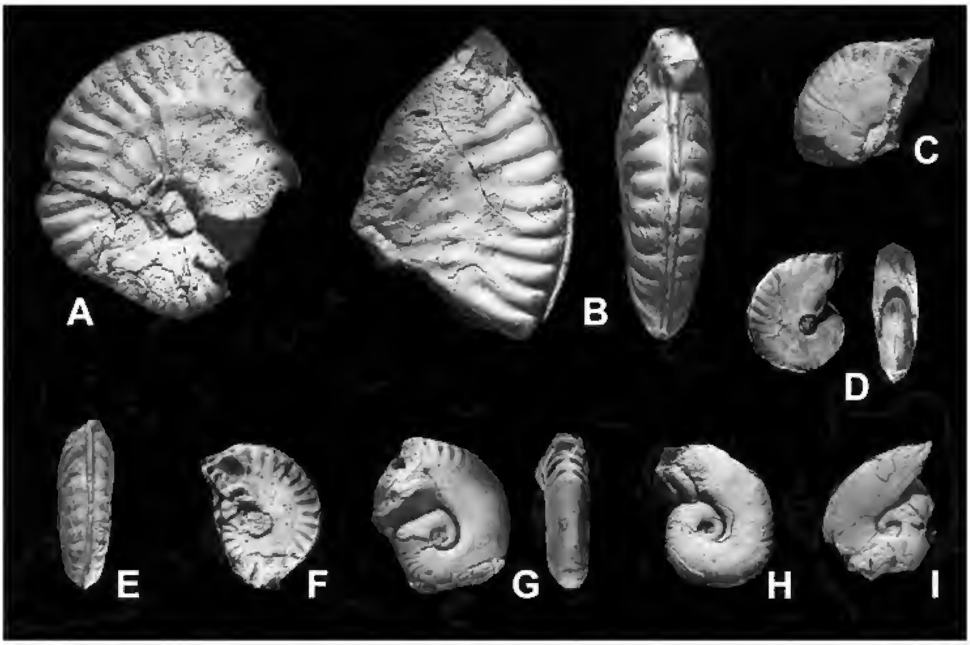


Fig. 16. **A–F** *Strigoceras symplectum* (Buckman) and **G–I** corresponding microconch dimorph *Cadomoceras nepos* (Parona); Upper Bajocian, Niortense Zone. **A, B, E, F.** West Turkmenistan, Great Balkhan Range, South of Porsaiman source; lower part of Tschaloi Formation; VNIGNI N 115/1985, N 115/7393, N 115/7390, N 115/1983. **C, D.** West Turkmenistan, Great Balkhan Range, South of Schorli source; lower part of Tschaloi Formation; VNIGNI N 115/7387, N 115/7391. **G, I.** West Turkmenistan, Great Balkhan Range, Karaiman source; lower part of Tschaloi Formation; NIGNI N 115/7287, N 115/7991. **H.** North Caucasus, Dagestan, section near the village Irganai; uppermost part of Kumuh Formation; VNIGNI N 115/7283. – ×1.

ly bordering the lateral furrows. This is shown clearly by Buckman's shell rubbings. The rather widely-spaced ribbing is slightly prorsiradiate, polyschizotome, most with one or two secondaries intercalated between longer primaries. The ventral ends of the secondaries are truncated. Although the oxycone cross section is comparatively slender, the median longitudinal furrow is prominent. In large specimens weak furrows around the umbilicus are developed ventrally to the median furrow. This is seen due to a weakening of the striation in the furrows. In *S. symplectum* thicker specimens with coarse ribbing persisting to the innermost whorls occur rather frequently within the variability of the species.

◀ **Fig. 15.** *Strigoceras symplectum* (Buckman), lateral and ventral views. **A.** Bisingen-Zimmern near Balingen, SW Germany; Ostreenkalk Formation, Subfurcatenoolith Member, Upper Bajocian, Niortense Zone; SMNS 67157 (leg. R. Hugger). **B.** La Jeandonnière, Dept. Vendée, France; Upper Bajocian, ?Niortense or Garantiana Zone; SMNS 65378 (Coll. G. Schweigert). – ×1.

Measurements

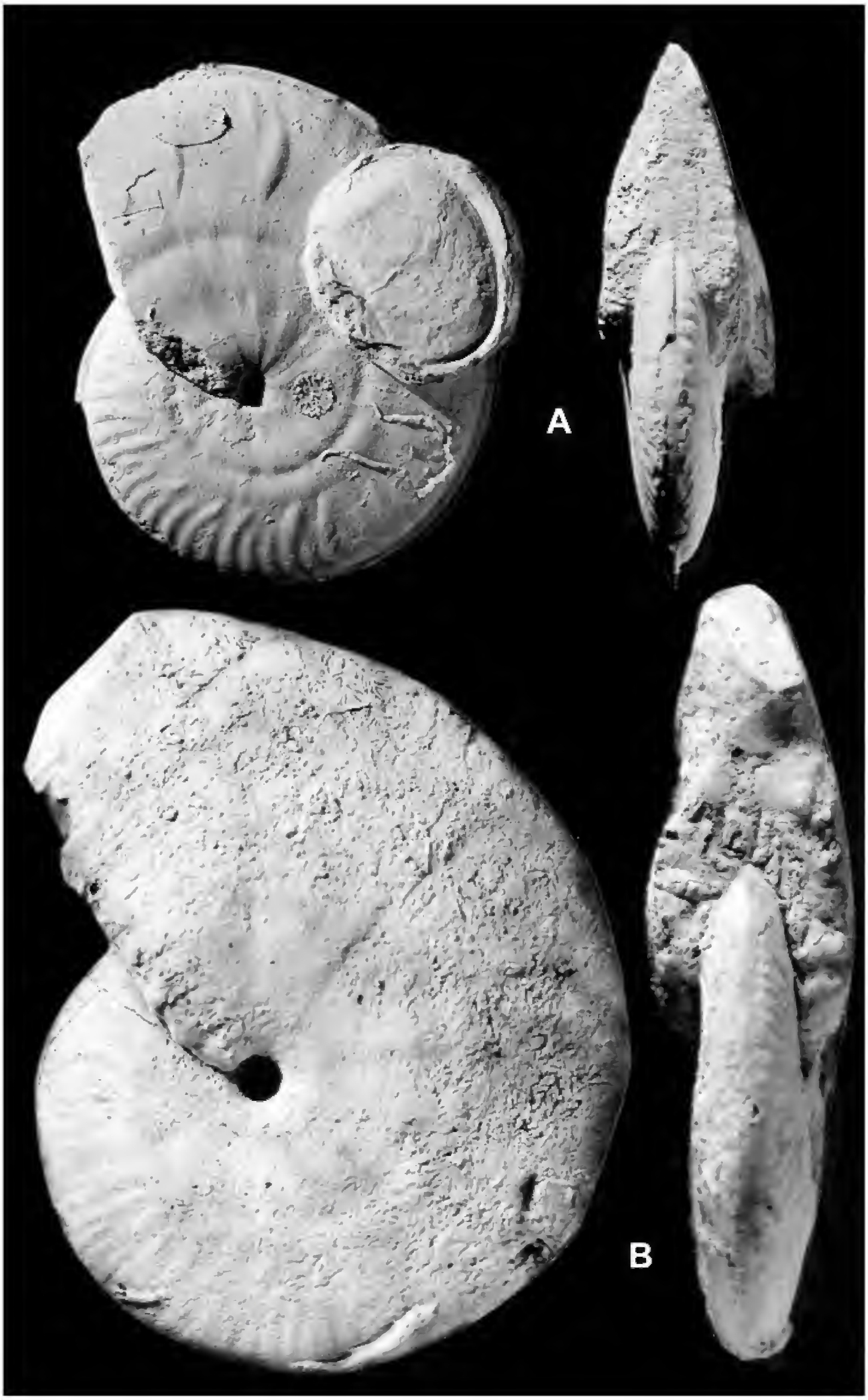
	d	h	w	u	r/2	h/d	w/d	u/d
GSM 37319 (holotype)	91.0	53.5	20.0	4.5	25	0.59	0.22	0.05
SMNS 65371 (Fig. 14A)	58.0	30.7	14.3	5.5	20	0.53	0.25	0.09
SMNS 65378 (Fig. 15B)	85.0	50.0	22.5	4.1	29	0.59	0.26	0.05
SMNS 65377 (Fig. 13B)	95.0	54.3	22.5	4.8	36	0.57	0.24	0.05
SMNS 67157 (Fig. 15A)	99.0	57.0	25.7	5.8	24	0.58	0.26	0.06

Strigoceras septicarinatum (Buckman, 1924)

Figs. 17, 18A, 19

v pars 1886 *Ammonites Truellei.* – Quenstedt, p. 565, pl. 69, figs. 11–12 only.
1912 *Strigoceras Truellei,* Sowerby. – Roman & Gennevaux, p. 88, pl. 3, fig. 3.
v * 1924 *Strigites septicarinatus* nov. sp. – Buckman, pl. 470.
? 1927 *Oppelia (Strigoceras) truellei* d'Orbigny. – Roman & Pétouraud, p. 50.
1953 *Strigoceras* sp. – Mouterde, p. 211.
v ? 1963 *Strigites pseudostrigifer.* – Wendt, p. 118, pl. 17, fig. 3.
pars 1964 *Strigoceras truellei.* – Rioult, p. 245.
1965 *Strigoceras truellei* (d'Orbigny). – Mensink, p. 82.
1968 *Strigoceras truellei.* – Pavia & Sturani, p. 314.
1970 *Strigoceras truellei* (d'Orb.). – Galácz, p. 119.
1970 *Strigoceras septicarinatum.* – Senior et al., p. 117.
1970 *Strigoceras compressum.* – Senior et al., p. 117.
v pars 1974 *Strigoceras truellei* (d'Orb.). – Dietl, table 1.
v pars 1975 *Strigoceras truellei* (d'Orbigny). – Hinkelbein, p. 156, tab.-figs. 11–12.
1982 *Strigoceras paronai.* – Fernández López, tab.-fig. 2.
1982 *Strigoceras truellei.* – Fernández López, tab.-fig. 2.
1983 *Strigites paronai* (Trauth). – Pavia, p. 69, pl. 8, fig. 3.
1983 *Strigoceras* sp. – Sandoval, tab.-figs. 21, 26, 36, 41, 48.
1983 *Strigoceras* cf. *truellei* (d'Orb.). – Sandoval, tab.-figs. 29, 48, 67.
1983 *Strigoceras truellei* (d'Orb.). – Sandoval, tab.-figs. 67, 68, 69, 77A.
1983 *Strigoceras paronai* (Trauth). – Sandoval, tab.-figs. 69, 77A.
v 1985 *Strigoceras septicarinatum* Buckm. 1924. – Schlegelmilch, pl. 21, fig. 2 (re-figuration of Buckman's holotype).
1986 *Strigoceras* cf. *pseudostrigifer* (Maubeuge, 1955). – Sandoval & Westermann, p. 1230, pl. 12, figs. 3–4.
? 1987 *Strigoceras simplectum* (Buckm.). – Enay et al., p. 112.
1988 *Strigoceras septicarinatum.* – Fernández López & Aurell, tab.-fig. 4.
1990 *Strigoceras* sp. – Sandoval, tab.-fig. 3.
1991 *Strigoceras* sp. – Huxtable, p. 197.
1994 *Strigoceras* sp. – Sandoval, pl. 2, fig. 5.
1995 *Strigoceras paronai.* – Gauthier et al., p. 322.
1996 *Strigoceras symplectum.* – Gauthier et al., pl. 8, fig. 4.
1997 *Strigoceras.* – Rioult et al., p. 51.
1997 *Strigoceras* cf. *paronai.* – Fernández López et al., tab.-fig. 12.
1997 *Strigoceras* cf. *truellei.* – Fernández López et al., tab.-fig. 12.
1997 *Strigoceras trullei* (d'Orbigny 1845). – Schlampp, p. 194, fig. top right.
v ? 2000 *Strigoceras paronai.* – Besnosov & Mitta, pl. 1, figs. 5–6.
v 2002 *Strigoceras* sp. – Dietze et al., p. 40.
v 2002 *Strigoceras* sp. – Schweigert et al., p. 9.
2003 *Strigoceras truellei* (Orbigny). – Richter, p. 331, text-fig. bottom.
v 2004 *Strigoceras septicarinatum* (S. Buckman). – Dietze et al., p. 68.

Holotype: Buckman (1924, pl. 470), BGS GSM 37318, re-figured here as Fig. 17A.
Type locality: Burton Bradstock, Dorset, England.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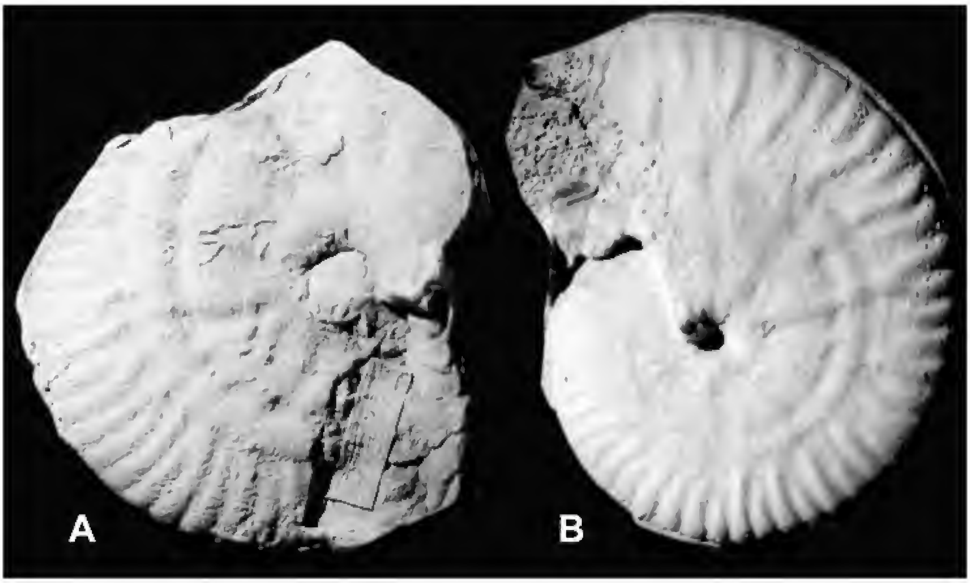

Fig. 18. A. *Strigoceras septicarinatum* (Buckman) var. *truellei* (d'Orbigny), lateral view; Villel, Keltiberian Ranges, E Spain; bed 19 in section E of Hinkelbein (1975, fig. 12), Upper Bajocian, Garantiana Zone; SMNS 65376 (Coll. K. Hinkelbein). **B.** *Strigoceras truellei* (d'Orbigny) var. *septicarinatum* Buckman, lateral view; Burton Bradstock, Freshwater Caravan Park; Inferior Oolite, Upper Bajocian, Parkinsoni Zone, Acris Subzone, *Parkinsonia rarecostata* horizon (= horizon Bj-26b of Callomon 1995); SM X.29151 (leg. D. Sole, ex RBC collection). – × 1.

Type horizon: Inferior Oolite, Shell Bed P. I of Buckman 1910 (Parkinsoni Zone, Acris Subzone, *rarecostata* horizon, see Dietze 2000; Chandler et al. 2001; Dietze et al. 2002).

Stratigraphic range: Garantiana Zone to early Parkinsoni Zone (Acris Subzone).

Studied material: 30 specimens.

Records: S Germany, Spain, France, England, Hungary, Southern Alps, Turkmenistan, Alaska (Wrangellia Terrane), Morocco, Mexico, ?Sicily.

Diagnosis. – *Strigoceras* with two well-developed lateral furrows separated by a marked ridge, extremely narrow umbilicus, juvenile sculpture strong, irregularly polyschizotome, lunulate secondary ribbing with a swollen point of bifurcation.

Description. – The holotype of *Strigoceras septicarinatum* (Buckman) is a small adult specimen with most of the striate shell preserved on both flanks. The specimen is a phragmocone with about one half whorl of bodychamber. One flank is encrusted by several serpulids and an oyster. The cross section is oxyconic with a low rounded keel. The umbilicus is extremely narrow. There are two lateral furrows developed parallel to an enclosed ridge. The primary ribs are very weak with

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Fig. 17. *Strigoceras septicarinatum* (Buckman), lateral and ventral views. **A.** Holotype. Burton Bradstock, Dorset, England; Inferior Oolite, Shell Bed P. I of Buckman 1910, Upper Bajocian, Parkinsoni Zone, Acris Subzone, *Parkinsonia rarecostata* horizon; BGS GSM 37318. **B.** Bopfingen-Oberdorf, SW Germany; Sengenthal Formation, Bifurcatenoolith Member, bed B3 in Dietze et al. (2002), Upper Bajocian, Garantiana Zone, Garantiana Subzone, *Garantiana subgaranti* horizon; SMNS 67158 (ex coll. V. Dietze). – × 1.

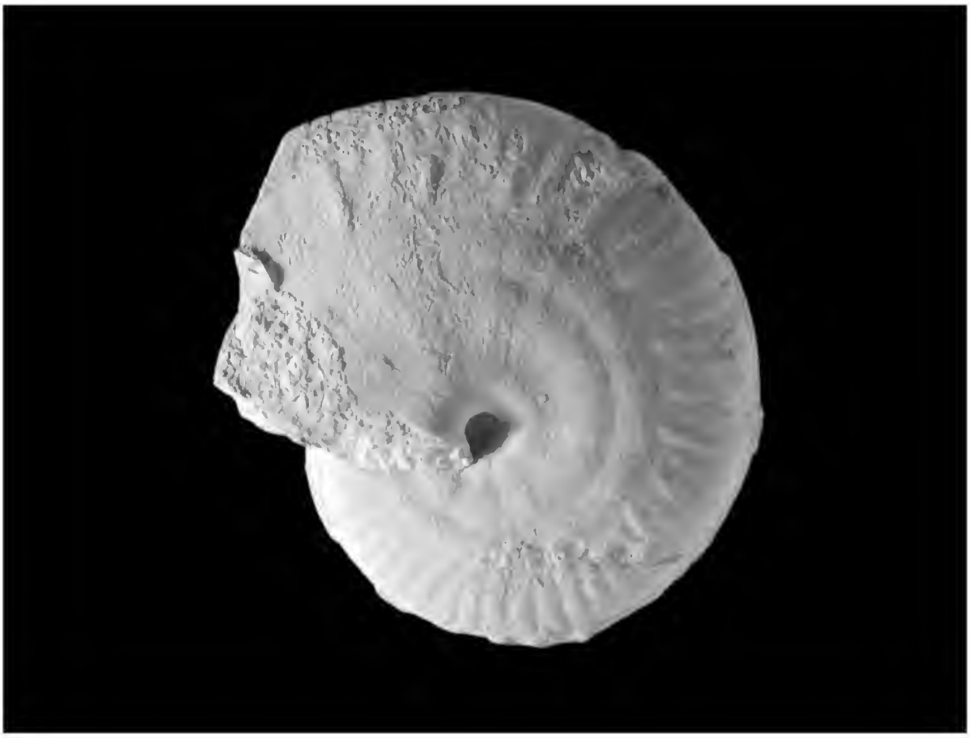


Fig. 19. *Strigoceras septicarinatum* (Buckman), lateral view; Southern Alaska, Talkeetna Mountains, Boulder Creek area, 26 km NE of Chickaloon (Imlay 1980: fig. 1, block 2), US co-ordinates Anchorage D-3 quadrangle, R7E, T22N, SE$^1/_4$; 148° 5′40″W, 61° 58′10″N; ca. 1 km E of Imlay's locality 17 (Imlay 1980: fig. 9); altitude ca. 1680 m; Tuxedni Group, lower Chinitna Formation (Wrangellia Terrane), Upper Bajocian, ?Garantiana Zone – Parkinsoni Zone, Acris Subzone; University of Alaska Museum, Fairbanks, AK, Earth Sciences, no. A 2489.11a (leg. J. H. Callomon & R. C. Allison). – Diameter of specimen 110 mm.

stronger secondaries that are falcoid, with some swollen bifurcation points. On the bodychamber these become weak, with some retaining a swollen crescent ornament. In larger specimens the ribbing resembles that of the phragmocone of the holotype, but persists later in ontogeny.

Comparisons. – *S. septicarinatum* (Buckman) represents a direct phyletic ancestor of *S. truellei* differing from it in possessing a generally more slender whorl section and stronger lateral furrows. Nodular swelling of the primaries is very typical of this chronospecies, otherwise seen only in some coarsely ribbed variants of *S. truellei*. Within the variation of the chronospecies *S. septicarinatum* (Buckman) there are some morphologically transient forms in which swollen ribs only rarely occur, here treated as *S. septicarinatum* (Buckman) var. *truellei* (e.g. Fig. 18A). In the older chronospecies *S. symplectum* (Buckman), swollen primaries may occur only exceptionally in some extreme variants.

Identification of a well-preserved specimen of *S. septicarinatum* (Buckman) in a Middle Jurassic section of the Wrangellia Terrane in southern Alaska (Fig. 19) provides an estimate of the age. Soft shales with scattered fossiliferous concretions (Tuxedni Group, lower Chinitna Formation) occur at levels probably equivalent to

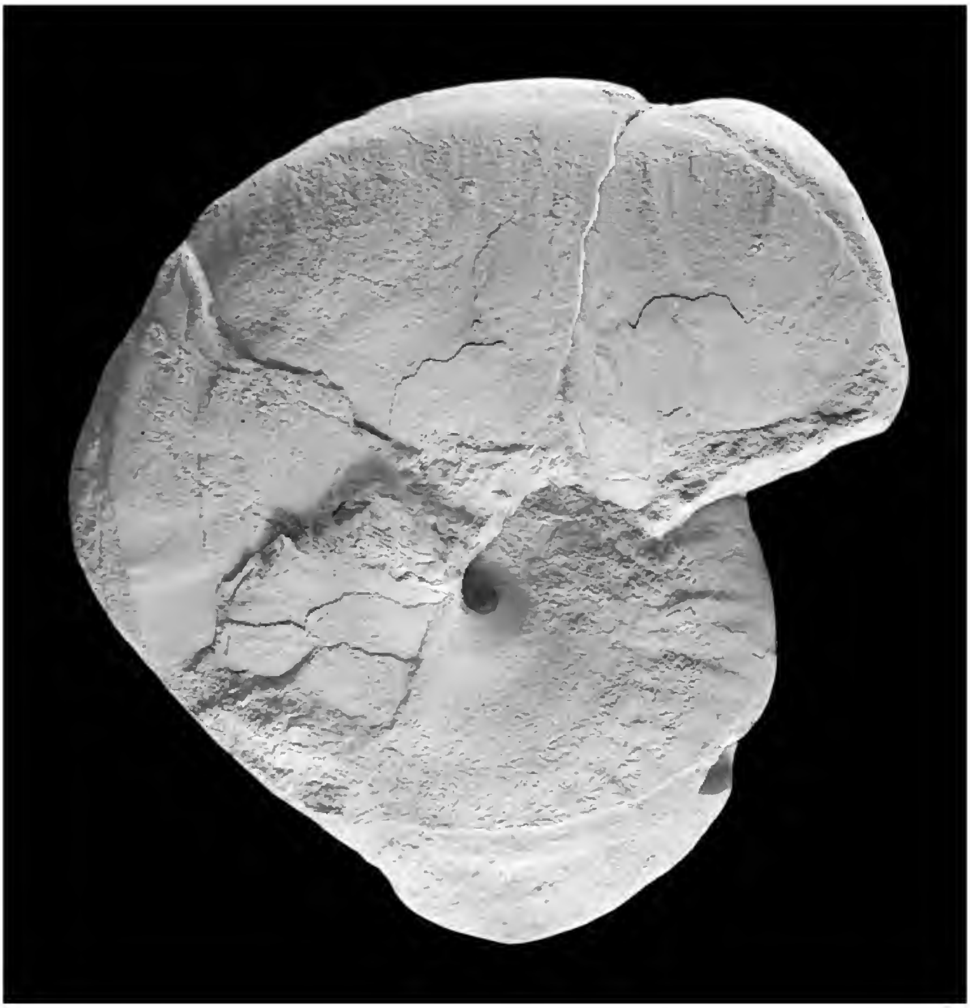


Fig. 20. *Oxycerites* cf. *aspidoides* (Oppel), lateral view; same locality and bed as Fig. 19. University of Alaska Museum, Fairbanks, AK, Earth Sciences, no. A 2489.10 (leg. J. H. Callomon & R. C. Allison). – Diameter of specimen 140 mm.

the upper part of the *Cranocephalites costidensus* Beds in Imlay's section (see Imlay 1980, fig. 4). The specimen was found together with *Oxycerites* cf. *aspidoides* (Oppel) (Fig. 20). The lectotype of *Oxycerites aspidoides* comes from the Upper Bajocian, late Parkinsoni Zone, of SW Germany (Dietl 1982). This *Strigoceras* is recorded as being slightly older, the equivalent of the Garantiana Zone or at least Acris Subzone of the early Parkinsoni Zone.

Measurements

	d	h	w	u	r/2	h/d	w/d	u/d
GSM 37318 (holotype)	74.5	44.5	19.0	1.5	~25	0.60	0.26	0.01
SMNS 67158 (Fig. 17B)	104.7	57.0	28.2	4.3	28	0.54	0.27	0.04

Strigoceras truellei (d’Orbigny, 1845)

Figs. 18B, 21–24

v *1845 *Ammonites Truellei.* – d’Orbigny, pl. 117, figs. 1–3 (= lectotype), pl. 129, figs. 1–2.
1856 *Ammonites Truellei* d’Orb. 1845. – Oppel, p. 492.
v 1857 *Ammonites truellei.* – Quenstedt, p. 525, pl. 69, fig. 23.
1860 *Ammonites Truellei* d’Orbigny 1845. – Ooster, p. 61.
v non 1865 *Ammonites Truellei* Orbigny. – Schloenbach, p. 173, pl. 3, fig. 2 (= *Phlycticeras dorsocavatum* (Quenstedt), see Schweigert & Dietze 1998).
pars 1878 *Amaltheus Truellei.* – Neumayr, p. 68.
1878 *Oppelia Truellei* d’Orbigny, sp. – Bayle, pl. 89, figs. 1, 3–4.
1884 *Amaltheus Truellei.* – Douvillé, pp. 34–35, text-fig. 16.
v pars 1886 *Ammonites Truellei.* – Quenstedt, p. 565, pl. 69, fig. 7 only.
v pars 1886 *Ammonites Truellei trifurcatus.* – Quenstedt, pl. 69, fig. 8 only [Fig. 21B].
1893 *Strigoceras Truellei.* – Buckman, p. 487.
1896 *A. Truellei* d’Orb. – Koken, p. 648.
1906 *Strigoceras Truellei* d’Orb. – Lissajous, p. 694.
1908 *Amaltheus (Strigoceras) Truellei.* – Engel, pp. 329, 340.
1910 *Strigoceras truellei.* – Buckman, pp. 55, 73.
? 1923 *Strigoceras Truellei* d’Orb. sp. – Trauth, p. 228. – [1923a].
v 1924 *Strigoceras truellei* d’Orbigny sp. 1846. – Buckman, pl. 472.
v 1924 *Strigoceras gracile* Quenstedt sp. – Buckman, pl. 585.
v 1928 *Strigoceras Truellei* d’Orb. – Scheurlen, p. 7, pl. 1, figs. 5, 7–11.
1935 *Strigoceras Truellei* d’Orb. sp. – Bircher, p. 133, tab. D.
v 1938 *Strigoceras Truellei* d’Orb. – Roman, pl. 17, fig. 178. – [re-figuration of holotype]
1939 *Strigoceras symplectus.* – Roché, p. 166.
1939 *Strigoceras septicarinatus.* – Roché, p. 166.
1952 *Strigoceras truellei.* – Kumm, p. 430.
1955 *Strigoceras truellei* (d’Orb.). – Westermann, p. 521.
1956 *Strigoceras truellei.* – Arkell, p. 366.
1957 *Strigoceras truellei* (Orb.). – Arkell, p. L272, text-fig. 314.1.
1958 *Strigoceras* aff. *truellei* (d’Orb.). – Wilson et al., p. 91.
1961 *Strigoceras truellei* (d’Orbigny). – Dollfuss, p. 95, pl. 2, fig. 4.
v 1963 *Strigoceras kuznetsovi* sp. nov. – Krymholtz & Stankevitch, p. 112, pl. 1, figs. 6–7.
1964 *Strigoceras truellei* (d’Orbigny). – Sturani, pl. 2, fig. 1. – [1964a].
1964 *Strigoceras truellei* (d’Orbigny). – Sturani, p. 37, pl. 5, fig. 6. – [1964b].
1964 *Strigoceras truellei.* – Hölder, p. 90.
1964 *Strigoceras truellei.* – Rioult, p. 246.
1968 *Strigoceras truellei.* – Pavia & Sturani, p. 315.
non 1969 *Strigoceras septicarinatum* (Buckman). – Mihajlovic, p. 61, pl. 2, fig. 6, pl. 3, fig. 1 (= *Prohecticoceras bisculptum* (Oppel), see Galácz 1999: 156).
1969 *Strigoceras gracilis* (Quenstedt). – Torrens, p. 327.
1969 *Strigoceras septicarinatus* S. S. Buckman. – Torrens, p. 327.
1970 *Strigoceras* cf. *truellei* (d’Orb.). – Galácz, p. 119.
1970 *Strigoceras septicarinatum* (Buckman). – Senior et al., pp. 114, 117.
1970 *Strigoceras truellei* (d’Orb.) – Senior et al., p. 116.
1970 *Strigoceras compressum* Etheridge. – Senior et al., p. 117.
1971 *Strigoceras truellei* (d’Orb.). – Rioult, p. 380.
1971 *Strigoceras truellei* (d’Orb.). – Sturani, p. 69.
1971 *Strigoceras truellei* (d’Orbigny). – Krystyn, p. 498.
1972 *Strigoceras truellei* (d’Orbigny). – Krystyn, p. 246, text-fig. 15.
pars 1973 *Strigoceras truellei.* – Pavia, table 3.
v 1977 *Strigoceras truellei.* – Dietl, p. 16.
v 1977 *Strigoceras truellei* d’Orb. – Benetti, p. 232, text-figs. 10–11.
1978 *Strigoceras* sp. – Sequeiros et al., p. 297.

1980 *Strigoceras truellei.* – Galácz, p. 55.
1982 *Strigoceras truellei* (Orbigny). – Richter, text-fig. 143.
1983 *Strigoceras truellei* (d'Orb.). – Sandoval, p. 123, tab.-figs. 8, 20, 21, 77A.
v 1985 *Strigoceras truellei.* – Rostovtsev, pl. 34, figs. 8–9.
pars 1985 *S. (Strigoceras) truellei* (d'Orbigny, 1845). – Sandoval, p. 98, pl. 2, fig. 3, non fig. 4 [= *S. paronai*].
1985 *Strigoceras septicarinatum* (Buckman). – Fernández López, pl. 13, fig. 5.
v 1985 *Strigoceras truellei* (d'Orb. 1845). – Schlegelmilch, pl. 20, fig. 5.
1987 *Strigoceras truellei.* – Doré et al., pl. 5, fig. 6.
1987 *Strigoceras symplectum.* – Enay et al., p. 112, tab.-fig. 2.
1988 *Strigoceras septicarinatum* (Buck.). – Fernández López, p. 78.
1988 *Strigoceras truellei* (Orbigny). – Gómez-Alba, pl. 208, fig. 1.
1990 *Strigoceras truellei.* – Sandoval, pl. 4, fig. 7.
v 1992 *Strigoceras truellei* Orb. – Rostovtsev, pp. 106, 134.
v 1994 *Strigoceras truellei.* – Rioult et al. in Fischer, pl. 50, figs. 1–2.
1995 *Strigoceras truellei* (d'Orbigny). – Callomon & Cope, p. 65.
1995 *Strigoceras septicarinatus* Buckman. – Callomon & Cope, p. 66.
1997 *Strigoceras truellei* (d'Orb.). – Rioult et al., pl. 15, fig. 7.
1998 *Strigoceras compressum.* – Pavia & Martire, p. 173.
1998 *Strigoceras septicarinatum.* – Pavia & Martire, p. 173.
v 1999 *Strigoceras truellei.* – Schweigert & Dietze, p. 55.
v 2001 *Strigoceras truellei* (d'Orb. 1845). – Arp, p. 214, pl. 6, fig. 4.
2002 *Strigoceras truellei* (d'Orbigny). – Di Stefano et al., p. 288.
2002 *Strigoceras* cf. *septicarinatum* (Buckman). – D'Arpa in: Pavia & Cresta, p. 199, fig. 131.
2002 *Strigoceras truellei* (d'Orbigny, 1845). – Schlögl, pl. 15, fig. 1.
v 2003 *Strigoceras truellei.* – Chandler & Dietze, p. 39.
2004 *Strigoceras (Strigoceras).* – Zatoń & Marynowski, p. 342.
2005 *Strigoceras truellei* (d'Orbigny, 1845). – Schlögl et al., p. 343, pl. 3, fig. 4.
2006 *Strigoceras (Strigoceras)* sp. indet. juv. gr. *strigifer/pseudostrigifer.* – Zatoń & Marynowski, p. 435, fig. 3.14.
v 2006 *Strigoceras truellei* (d'Orbigny). – Dietze & Dietl, p. 10, fig. 6.

Lectotype: d'Orbigny (1845, pl. 117, figs. 1–3) MNHN IPM-R 4117 (coll. d'Orbigny no. 2135-1), designated as "holotype" by Rioult et al. in Fischer (1994: 103); re-figured here as Fig. 21A. This specimen is very close to the illustration of d'Orbigny's specimen, although there are 3 syntypes in d'Orbigny's collection. Hence the "holotype" may be considered as a lectotype.

Type locality: Vicinity of Bayeux, Calvados, France.

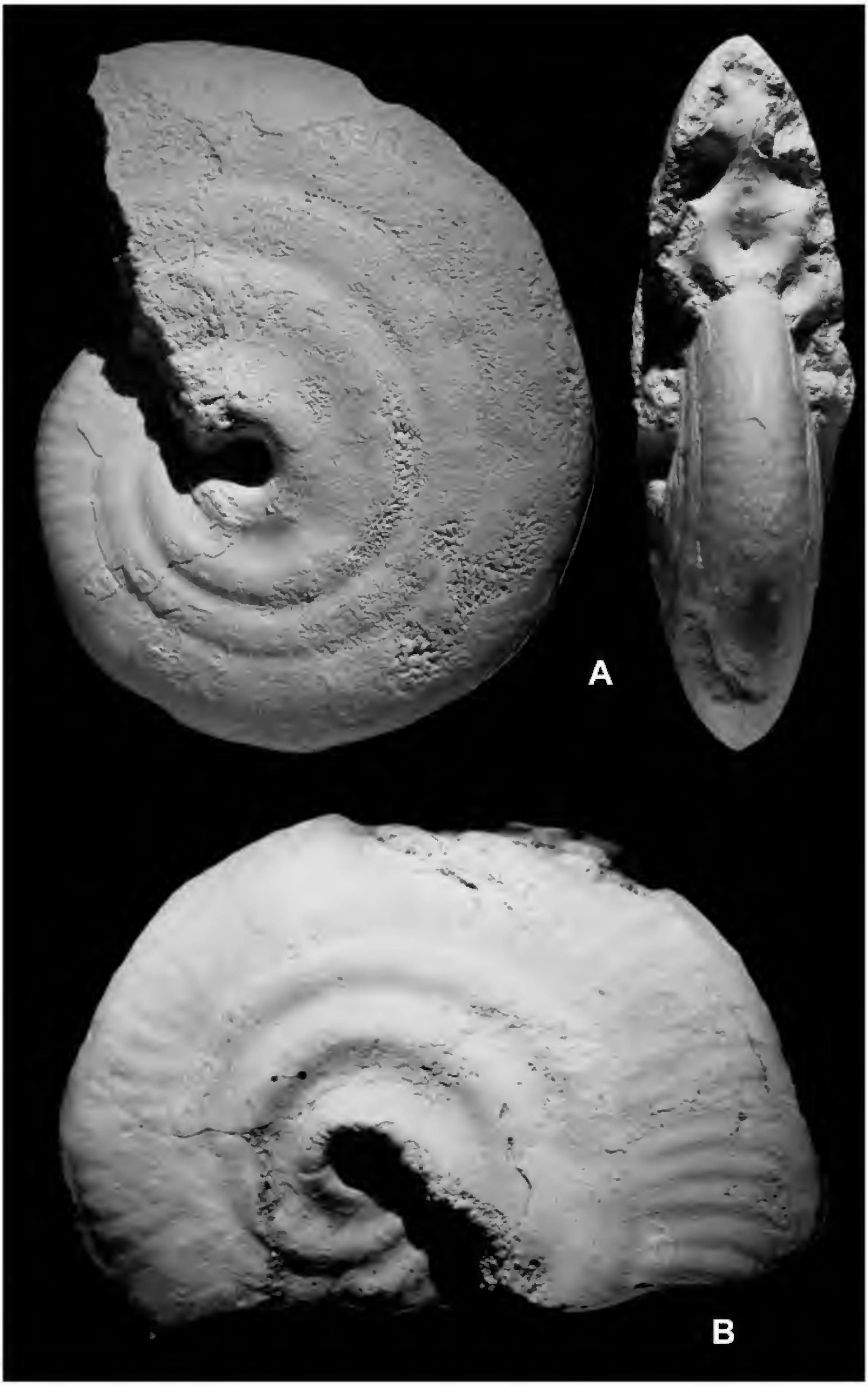
Type horizon: Oolithe ferrugineuse de Bayeux (Late Bajocian, Parkinsoni Zone, Truellei Subzone).

Stratigraphic range: Middle Parkinsoni Zone (Truellei Subzone) – late Parkinsoni Zone (Bomfordi Subzone).

Studied material: Ca. 25 specimens.

Records: France, England, SW Germany, Central Poland, Switzerland, S Spain, Southern Alps, Eastern Alps, Carpathians, W Sicily, Hungary, Caucasus.

Fig. 21. *Strigoceras truellei* (d'Orbigny). **A.** Lectotype, lateral and ventral views; surroundings of Bayeux, France; Oolithe ferrugineuse de Bayeux, Upper Bajocian, Parkinsoni Zone; MNHN IPM-R 4117 (coll. d'Orbigny no. 2135-1). **B.** Original specimen of *Ammonites truellei trifurcatus* Quenstedt 1886, pl. 69, fig. 8, lateral view; according to lithology not coming from "Oberer Brauner Jura delta of Geisingen" as indicated on the label and in the publication, but from the Sengenthal Formation, Parkinsonienoolith Member of the Ipf area in eastern Swabia; Upper Bajocian, Parkinsoni Zone, Truellei Subzone; IFGT, Quenstedt collection, without number. – A: ×2/3, B: ×0.5. ▶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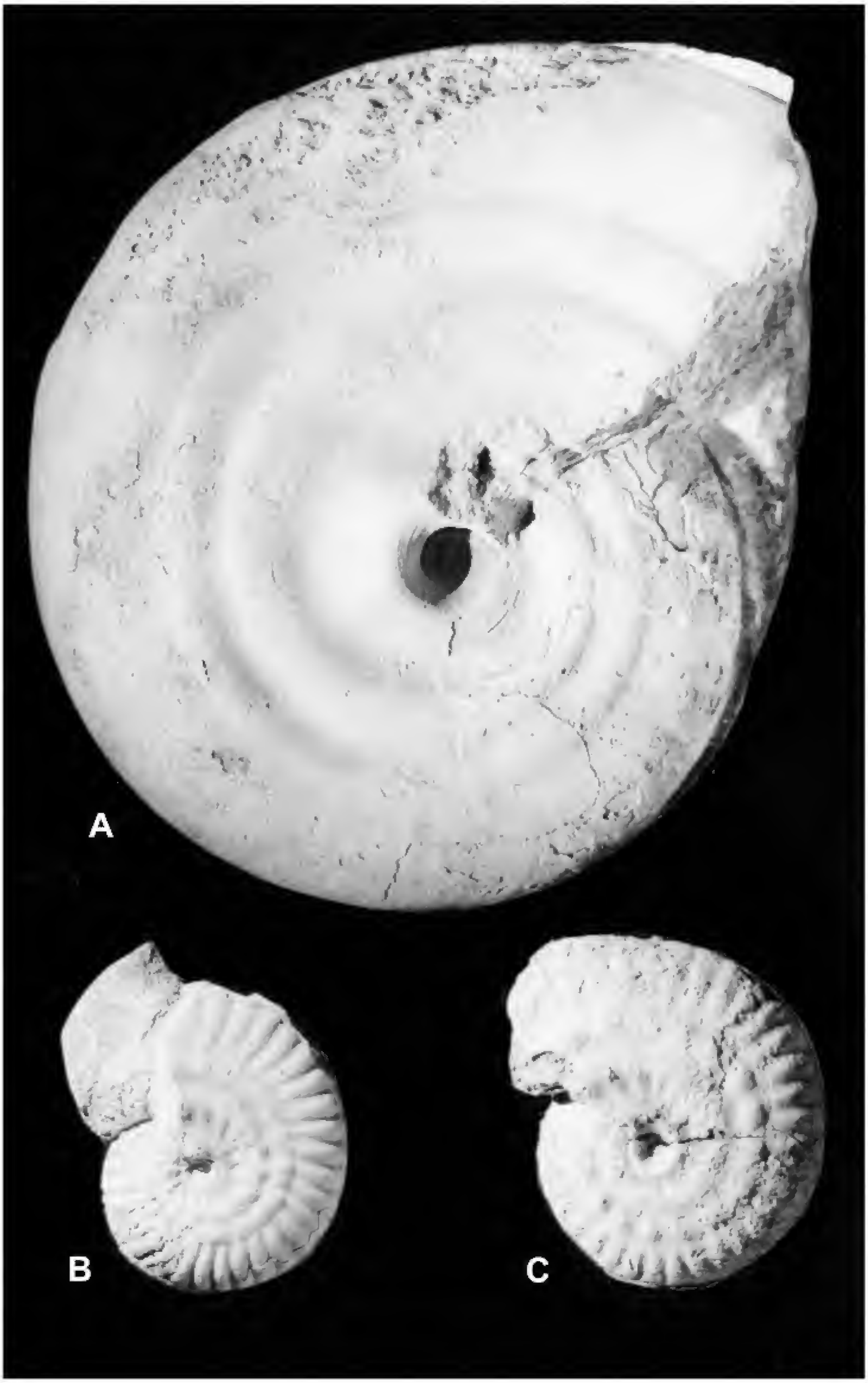
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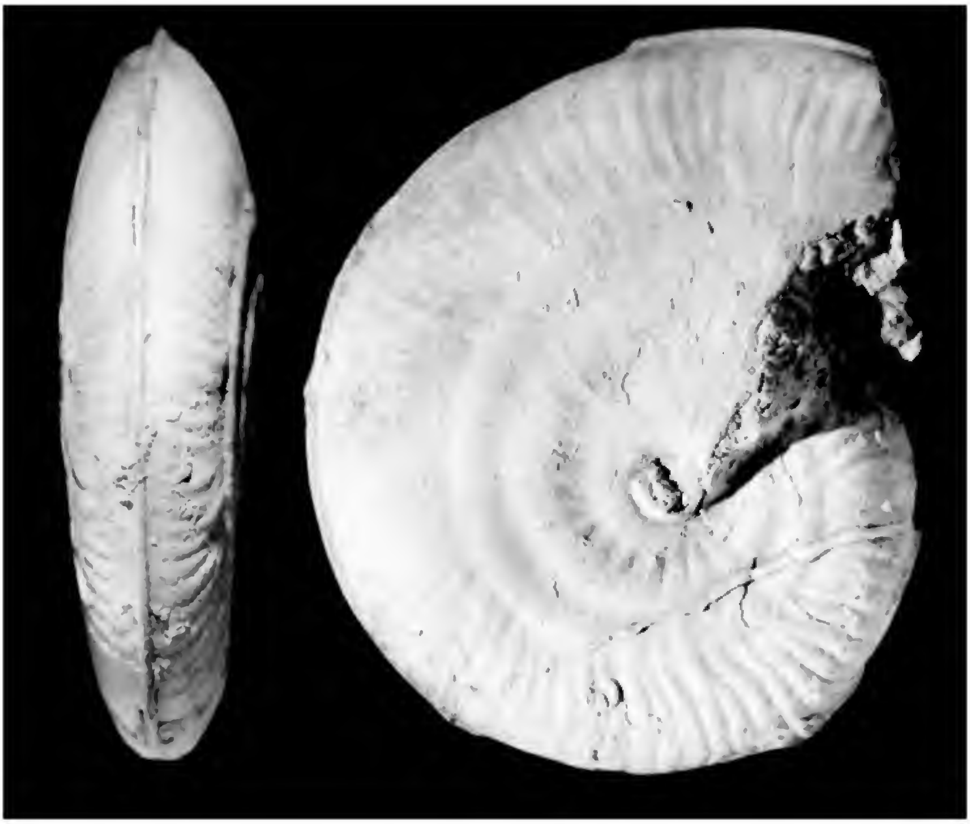

Fig. 23. *Strigoceras truellei* (d'Orbigny), ventral and lateral views of a relatively slender and fine-ribbed specimen; Burton Bradstock, beach exposure; Inferior Oolite, Truellei Bed (bed 13 b of Callomon & Chandler 1994), Upper Bajocian, Parkinsoni Zone, Truellei Subzone, *Parkinsonia parkinsoni* β horizon; SM X40234 (ex RBC collection). – × 1.

Diagnosis. – *Strigoceras* showing three well-developed lateral furrows or depressions. It attains the broadest shell morphology for the genus.

Description. – For details see Rioult et al. (1994). The lectotype of *S. truellei* is a relatively large, completely septate, discoid phragmocone with remnants of the shell. The umbilicus is extraordinarily deep with a steep but rounded umbilical shoulder. Three longitudinal furrows are developed, the umbilical one being the broadest. The low, rounded keel is not preserved in the lectotype. The sculpture

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◀ **Fig. 22.** *Strigoceras truellei* (d'Orbigny). **A.** Lateral view. Burton Bradstock, Dorset, beach exposure; Inferior Oolite, Truellei Bed (bed 13 b of Callomon & Chandler 1994), Upper Bajocian, Parkinsoni Zone, Truellei Subzone, *parkinsoni* β horizon; SMNS 67159 (ex coll. V. Dietze). **B.** Lateral view; same locality and horizon as Fig. A; SMNS 65381 (ex coll. N. Schaffeld). **C.** Lateral view (= original specimen figured by Dietze & Dietl 2006, fig. 6). Bopfingen, SW Germany, Oberer Kreuzheckenweg; Sengenthal Formation, Parkinsonienoolith Member, Upper Bajocian, Parkinsoni Zone, Truellei Subzone; SMNS 66129 (leg. H.-D. Bolter). – × 1.

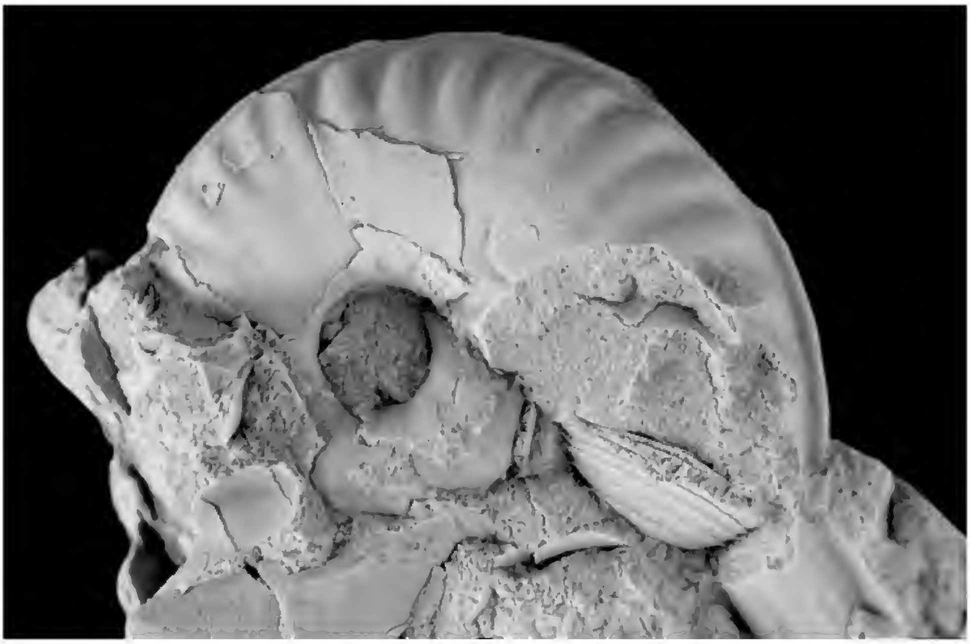

Fig. 24. *Strigoceras truellei* (D'ORBIGNY), juvenile specimen; Kawodrza Górna (brick-pit "Sowa") near Czêstochowa, Central Poland; Upper Bajocian, Parkinsoni Zone, Bomfordi Subzone; GIUS-8-2456. – Diameter of specimen 14.3 mm.

consists of weak or feeble primaries and stronger, slightly prorsiradiate secondaries. One primary rib usually gives rise to three secondaries. The shell is smooth anterior to the last half of the outer whorl.

Comparisons. – Compared to many older chronospecies, *S. truellei* is quite common in the "Truellei Beds" of N France and S England. The great variability from compressed to stout forms is clearly due to the large sample size. Nevertheless we did not find any of the older chronospecies equivalent in the broadness of the shell. The development of three lateral furrows is clearest in the broader and larger specimens, in which the umbilical wall is slightly overhanging. Some specimens are already adult at a small diameter. These have a minute umbilicus and distinct nodular primaries strongly resembling those in the ancestral *S. septicarinatum* (BUCKMAN). These specimens may be taxonomically treated as a *septicarinatum* variety of *S. truellei* (e.g. Fig. 18B). In coarsely ribbed specimens the lateral furrows are often "segmented" by crossing primaries.

The contemporaneous *Phlycticeras buckmani* (BRASIL) differs from slender specimens of *S. truellei* by possession of a different type of keel, a wider umbilicus and the lack of lateral furrows (SCHWEIGERT & DIETZE 2004).

Remarks. – A single juvenile specimen (Fig. 24) from Central Poland is the only record from that area (ZATOŃ & MARYNOWSKI 2004, 2006). It was associated with parkinsoniids (*P.* aff. *bomfordi* ARKELL, *P.* aff. *dorni* ARKELL), *Phylloceras* sp., *Nannolytoceras tripartitum* (RASPAIL), *Vermisphinctes* sp., *Lissoceras (Lissoceras) oolithicum* (D'ORBIGNY), and *Lissoceras (Microlissoceras) solitarium* ZATÓN & MARYNOWSKI. A specimen of the subzonal index *Parkinsonia bomfordi* ARKELL was also recorded from the same bed and locality (MATYJA & WIERZBOWSKI 2000). These data suggest an age of Bomfordi Subzone of the Parkinsoni Zone. This is therefore the only hitherto documented *Strigoceras* of this age.

Strigoceras kuznetsovi KRYMHOLTZ & STANKEVITCH was recorded from the Late Bajocian or earliest Bathonian of Dagestan. Both syntypes of this species represent nuclei or juvenile specimens that do not differ significantly from nuclei of true *S. truellei* (D'ORBIGNY) so that a specific separation of this taxon seems arbitrary.

Measurements

	d	h	w	u	r/2	h/d	w/d	u/d
MNHN, IPM-R 4117 (lectotype)	158.5	89.5	42.0	10.0	(–)	0.56	0.26	0.06
SMNS 66129 (Fig. 22C)	55.0	29.5	18.8	4.0	19	0.54	0.34	0.07
SM X40234 (Fig. 23)	100.0	58.0	28.0	7.0	38	0.58	0.28	0.07
SMNS 67159 (Fig. 22A)	139.0	81.2	~50	7.8	(–)	0.58	0.36	0.06

Strigoceras callomoni n. sp.

Fig. 25

? 2000 *Strigoceras* sp. – FERNÁNDEZ LÓPEZ, p. 48, tab.-fig. 2.
? 2000 *Phlycticeras dorsocavatum* (QUENSTEDT). – FERNÁNDEZ LÓPEZ, p. 48, pl. 1, fig. 8.

Holotype: Specimen illustrated on Fig. 25, housed in the SMNS, no. 65380 (leg. A. & D. BERGER, Wiesloch).

Derivation of name: In honour of Prof. Dr. JOHN H. CALLOMON, London, our friend and renown ammonitologist, who has instructed us in principles of stratigraphy, taxonomy, and nomenclature.

Type locality: St. Honorine-des-Pertes, Calvados, France.

Type horizon: The holotype is an ex-situ find, according to the lithology of the rock matrix coming from the middle limestone bed of the Couches de Passage Member (Zigzag Zone, Macrescens Subzone, see DUGUÉ et al. 1998, figs. 28, 31). The preservational state of the holotype of *S. callomoni* n. sp. excludes reworking of this specimen.

Stratigraphic range: Early Bathonian.

Studied material: 1 specimen (holotype).

Records: N France, ? SE Spain.

Diagnosis. – Almost smooth species of *Strigoceras*, with four lateral depressions.

Description. – The holotype is a phragmocone with preserved striate calcitic shell. The specimen is almost entirely filled with sparry calcite. Part of the bodychamber on the last preserved whorl was broken away prior to burial indicating the length of the bodychamber was about 230 degrees. The remains of the rock matrix consist of a greyish marly biopelmicritic limestone containing pyritic inclusions, suggesting the middle limestone bed of the "Couches de Passage". The cross section is discoidal. The keel is rounded (partly restored in the holotype). Although only weakly developed, four longitudinal depressions are present in the first half of the last whorl. The outermost one on the third quarter of the whorl height fades out in the preadult stage.

Comparisons. – *Strigoceras callomoni* n. sp. differs from the older *S. truellei* (D'ORBIGNY) by becoming smooth at a much earlier ontogenetic stage. Some extreme variants of *S. truellei* from the younger part of the Parkinsoni Zone already re-

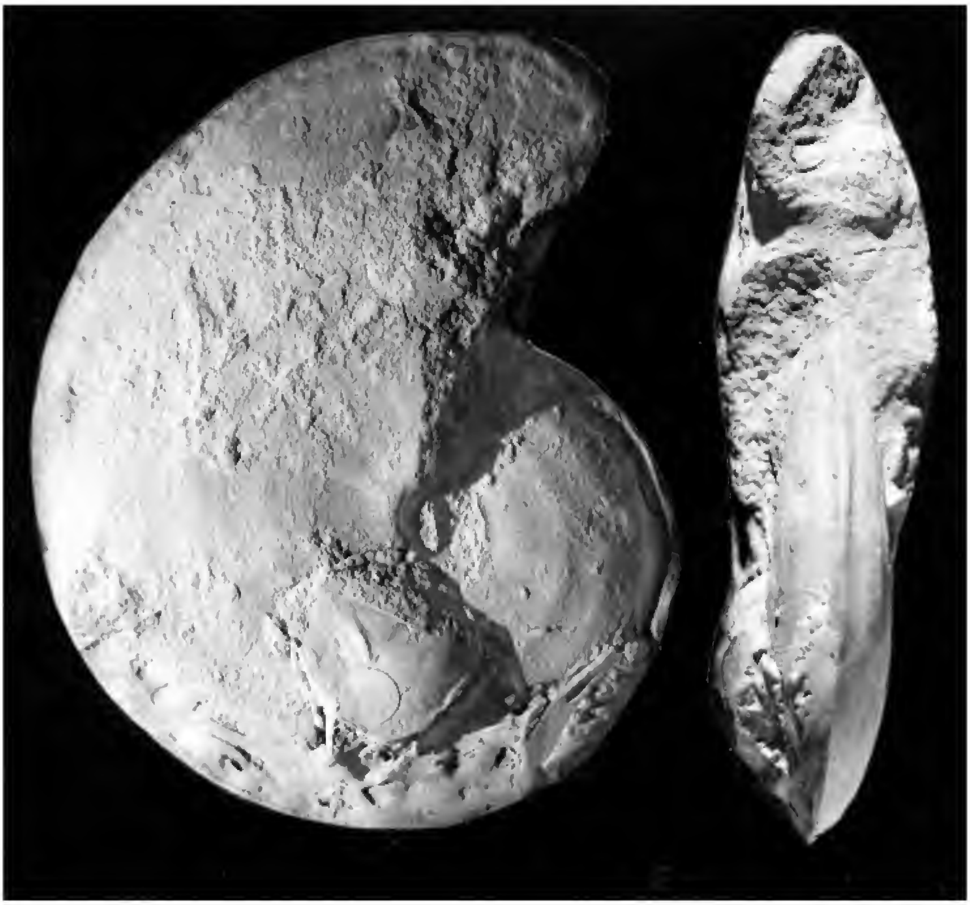

Fig. 25. *Strigoceras callomoni* n. sp., holotype, lateral and ventral views; St. Honorine-des-Pertes, Calvados, France; "Couches de Passage", most probably middle limestone bed, Lower Bathonian, Zigzag Zone, Macrescens Subzone, for stratigraphy see DUGUÉ et al. (1998, figs. 28, 31); SMNS 65380 (leg. A. & D. BERGER). – ×1.

semble *S. callomoni* n. sp. by their almost unribbed striate shell. The fourth lateral depression is unknown in other *Strigoceras* species. Only one specimen is available so we can say nothing about its intraspecific variability.

The juvenile specimen figured by FERNÁNDEZ LÓPEZ (2000, pl. 1, fig. 8) as "*Phlycticeras dorsocavatum*" lacks lateral spiral grooves but exhibits broad falcoid ribs. It most likely represents a *Strigoceras* rather than a *Phlycticeras*. In respect of its stratigraphical position (Parvum Subzone of Early Bathonian) this specimen could belong to *S. callomoni* n. sp., but it is not comparable with the holotype because of its minute size.

Measurements

	d	h	w	u	r/2	h/d	w/d	u/d
SMNS 65380 (holotype)	105.5	60.3	28.0	5.8	–	0.57	0.27	0.05

4. The phenomenon of dwarfism in adult macroconchs

The maximum adult size of macroconch strigoceratids is difficult to estimate because according to our observations to date not a single adult specimen has been found with an intact mouth border. However, there is evidence that surprisingly large specimens occur in almost all chronospecies. This is not only true for *S. truellei* from the Parkinsoni Zone of which large examples have been obtained quite frequently and more commonly than from other stratigraphical levels. We have studied very large specimens of *S. truellei* with diameters up to 290 mm that are still completely septate. This gives estimates of final adult diameters in these specimens of c. 500 mm. The main phyletic trend recognizable in *Strigoceras* is the predominance of broader specimens within the variation of the younger chronospecies, a phenommenon remarkably analogous in *Phlycticeras* (SCHWEIGERT & DIETZE 1998). Specimens with maximum ratios of width to diameter occur just prior to the extinction of the genus. The latest known chronospecies to date, *S. callomoni* n. sp., is the only example that contradicts this phyletic trend, but nothing is known about variation in size of this at present monotypic taxon.

Within a *Strigoceras* population that can be considered to be more or less isochronous some of the specimens show adult features but remain remarkably small, often skipping the second sculptural stage of ontogeny what is irregularly polyschizotome. Their final, smooth sculptural stage is the same as that of the large specimens. In the dwarf adults the suture lines are more complex at equal diameters to large adults and their umbilicus is extremely narrow. This observation led BUCKMAN (1924: 7) to distinguish several different genera within Strigoceratidae. In some faunas the number of dwarfs is very high, whereas in others the normal-size specimens dominate. Individuals therefore attain adulthood at very different sizes. In the micromorphic adults the rate of ontogenetic development appears accelerated, possibly as the result of local environmental changes. In early studies on strigoceratids this phenomenon was not recognized and small and large adult specimens were placed in different morphospecies or phyletic lineages (e. g. SANDOVAL 1985). Morphospecies taxonomically based on dwarf or small adults are *S. languidum* (BUCKMAN), *S. pseudostrigifer* MAUBEUGE, *S. bessinum* BRASIL, *S. egertense* OHMERT, GASSMANN, SCHATZ & STETTER, and *S. septicarinatum* BUCKMAN. The lectotype of *S. paronai* (TRAUTH) is a very small specimen that is not representative of the adult stage of this taxon (see above). Within a chronospecies there are adult forms varying from extremely small to very large supporting the idea that this phenomenon is more likely to be intraspecific variability than sexual polymorphism or specific diversification.

5. Shell structure of *Strigoceras*

Compared to *Phlycticeras*, stratigraphically younger representatives of *Strigoceras* do not show the spiral longitudinal striation on moulds. Only in a few cases is the striation superimposed on the mould during early diagenesis. Since most material is preserved in micritic limestones or ferrugineous oolites, the original aragonitic shell is very rarely preserved. If the shell is present, it mostly consists of re-crystallised calcite, thus few examples with partial aragonitic shell preservation could be studied. The spiral striation in *Strigoceras* is restricted to the medium nacreous layer of the shell but is lacking both in the inner and outer prismatic layers. In the inner prismatic layer, there are rows of minute tubercles arranged more or less radially, but in an irregular pattern. In calcite preservation the inner prismatic layer is usually recrystallised and welded to the nacreous layer. The distance between the rows of tubercles on the inner prismatic layer is the same as the width of the striae in the nacreous layer. This nacreous layer is striate, with dense striae each of equal size. The grooves between the striae fit exactly with the underlying tubercles of the inner prismatic layer. The nacreous layer is the thickest and hence often preserved. The outer prismatic layer is smooth. Originally it was covered by an organic periostracum that is never preserved due to a lack of specimens from bituminous shales. The outer prismatic layer was not preserved in the specimens studied by SCHEURLEN (1928), so this author erroneously observed *Strigoceras* to have only two shell layers.

The shell structure of *Strigoceras* does not differ principally from that of *Phlycticeras*; only the striate nacreous layer is more accentuated in the latter, so that the relatively thin inner and outer prismatic layers also takes on a striate overprint.

6. Possible phyletic descendants of *Strigoceras*

CALLOMON (in DONOVAN et al. 1981) interpreted the unique *Vastites vastus* ARKELL, 1951 from the Lower Bathonian of Doulting in Somerset as a late strigoceratid. To our knowledge, *Vastites* has never been recorded elsewhere besides the holotype. In the inner whorls the shell bears a striation (pers. comm. J. H. CALLOMON, London) not visible in the photographs provided by ARKELL (1951), and the cross-section shows a high, floored (septicarinate) keel. In addition, the ornament consisting of faint radial lirae resembles that of a lytoceratid. This may represent remains of the innermost shell layer (see above). The suture line is much simpler than that of *Strigoceras*. Lateral furrows are not developed on the flanks in the adult stage, but we cannot say anything of the nature of the inner whorls. A striation-like shell structure superficially resembling that of *Strigoceras* also occurs in other Middle Jurassic ammonite lineages (cf. SCHEURLEN 1928; JAWORSKI 1926, pl. 3, figs. 1c, 11; DORN 1935, pl. 23, fig. 2). ARKELL (1951) and MAUBEUGE (in ARKELL 1951) both suggested a sonniniid ancestry of *Vastites*. For the moment, the systematic position of *Vastites* within strigoceratids must remain doubtful.

The genus *Strungia* ARKELL, 1952 was indeed polyphyletic already when established. Its striate type species, *Oppelia redlichi* POPOVICI-HATZEG, represents an early offshoot of *Phlycticeras* in the Middle Bathonian and clearly belongs to Phlycticeratinae (SCHWEIGERT et al. 2003). Another "*Strungia*" described from Central Arabia (ARKELL 1952) exhibits falcoid ribbing. This unique "*Strungia*" *arabica* ARKELL displays a relatively wide umbilicus and hardly resembles a strigoceratid. It may be better interpreted as a microconch of the co-occurring genus *Micromphalites*. Also the Callovian species "*Strungia*" *voultensis* LISSAJOUS differs significantly from the characteristics of *S. redlichi* (see ELMI 1967) and represents a hecticoceratid.

In the Late Bajocian, or little earlier, the *Strigoceras* stock gave rise to the enigmatic genus *Granulochetoceras* GEYER, 1960 (Type species: *Ammonites uracensis* DIETLEN) via *Granulochetoceras oppeliisculptum* n. sp. from the Garantiana Zone, as demonstrated below. As a consequence, the stratigraphic range of Strigoceratinae extends from the Middle Aalenian to the Late Kimmeridgian, much longer than supposed in all previous phyletic trees of oppeliid relatives (e. g., ELMI 1967; DONOVAN et al. 1981).

Genus *Granulochetoceras* GEYER, 1960 [M]

Type species: *Ammonites uracensis* DIETLEN, 1911, by original designation.
Species included: *Ammonites argonautoides* MAYER, 1871; *Ammonites uracensis* DIETLEN, 1911; *Ochetoceras cristatum* DIETERICH, 1940; *Oppelia (Petitclercia ?) hungarica* LÓCZY, 1915 (Fig. 26B); *Granulochetoceras oppeliisculptum* n. sp. (Fig. 26A, this paper); *Ochetoceras ornatum* BERCKHEMER & HÖLDER, 1959; *Granulochetoceras undulatum* HÖROLDT, 1964).

Emended diagnosis. – Small to medium-size oxyconic ammonite; shell with spiral strigation; narrow umbilicus; steep umbilical wall; rounded umbilical edge; one or two lateral furrows; falcoid ribbing, primaries starting from nodules at umbilical edge; secondaries starting from strong bases; ribs do not reach keel; serrate, partly undulating septicarinate keel.

Granulochetoceras oppeliisculptum n. sp.
Fig. 26A

v pars 1974 *Strigoceras languidum* (BUCKMAN). – DIETL, table 1.

Holotype: Specimen illustrated in Fig. 26A, SMNS 65379 (leg. G. DIETL).
Derivation of name: After the ribbing style of the pre-mature growth stage strongly resembling that of an oppeliid.
Type locality: Aldea del Pinar, Keltiberian Ranges, NE Spain (see DIETL 1974).
Type horizon: Bajocian, Garantiana Zone, probably Dichotoma Subzone.
Stratigraphic range: Only recorded from the type horizon.
Studied material: Only holotype.
Records: Spain.

Diagnosis. – Oxyconic strigoceratid with oppeliid premature ribbing stage, low septicarinate keel with serrate venter; adult stage with polyschizotome ribbing.

Description. – The holotype is an internal mould of the phragmocone with remains of the shell. Its matrix consists of a light brown limestone with scattered small ferrugineous ooids. The keel is relatively low and laterally unsculptured, similar to typical *Strigoceras*, but at the beginning of the last whorl it is discernible that the shell covering the venter was serrate. The latter feature contradicts the diagnosis of *Strigoceras*. Therefore, it is included here in *Granulochetoceras*. This enigmatic genus was originally described from the Early Kimmeridgian of Southern Germany and Eastern France (see p. 48).

The inner whorls of the holotype are not visible because of the extremely narrow umbilicus. In all ontogenetic stages the conch is oxyconic. Up to a diameter of c. 50 mm falcoid ribs are developed, the primaries being relatively weak, the secondaries starting at mid-height of the flank. The bases of the secondaries are little swollen. In the ventral part of the flank each secondary is followed by two or three tertiary ribs. The ribs never reach the keel. At larger diameters the ribbing changes gradually to a more polyschizotome style as in coeval *Strigoceras*. On the flank two weak lateral

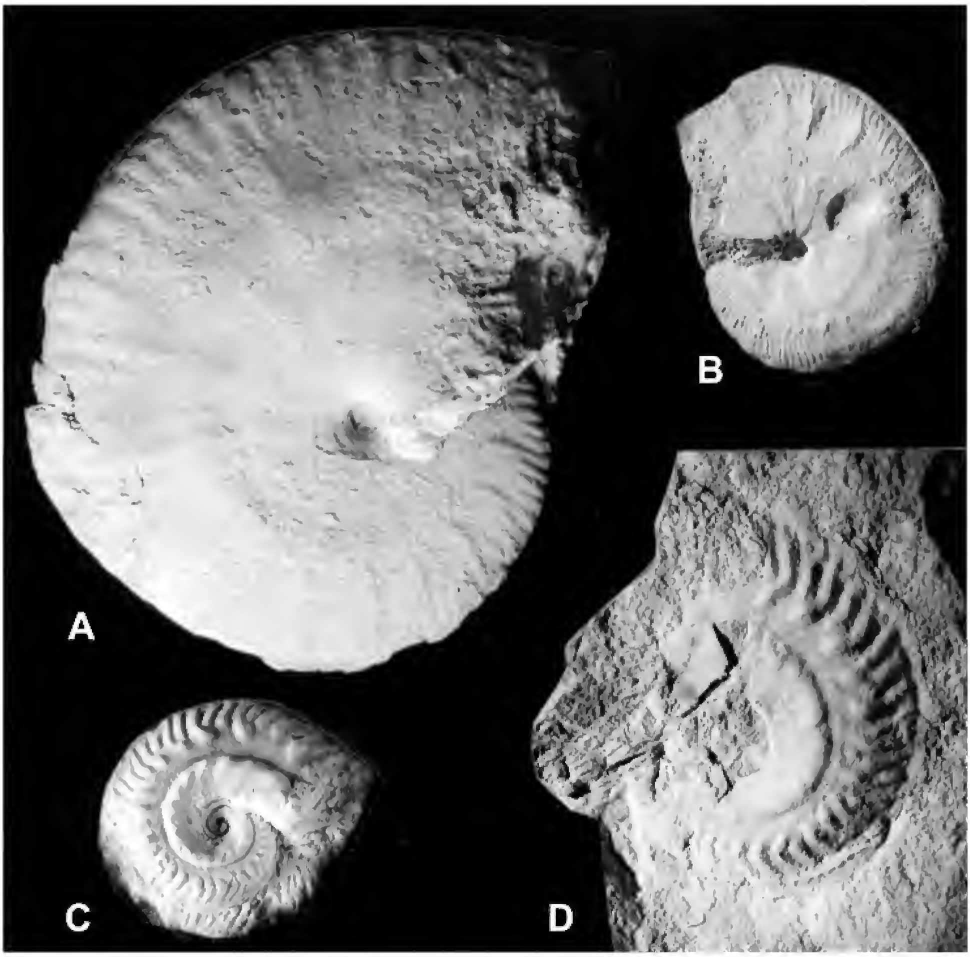

Fig. 26. **A**. *Granulochetoceras oppeliisculptum* n. sp., holotype, lateral view; Aldea del Pinar, NE Spain (for locality see DIETL 1974); Upper Bajocian, Garantiana Zone, probably Dichotoma Subzone; SMNS 65379 (leg. G. DIETL). **B**. *Granulochetoceras hungaricum* (LÓCZY), lateral view; Herznach iron mine, Herznach, Switzerland; "Anceps-Athleta-Schichten", Upper Callovian, Athleta Zone; NHMB J 19643 (leg. F. JENNY). **C**. *Granulochetoceras argonautoides* (MAYER), lateral view; Wasserberg near Schlat, E Swabia, SW Germany; Lacunosamergel Formation, Lower Kimmeridgian, Divisum Zone; SMNS 65359. **D**. *Granulochetoceras argonautoides* (MAYER), lateral view, showing the striation on the flank; Gruibingen, E Swabia, SW Germany; Lacunosamergel Formation, Lower Kimmeridgian, probably Divisum Zone; IFGT 1905-1. – A–C: ×1; D: ×1.5.

furrows or depressions are developed, the inner one being slightly stronger than the outer. A further shallow depression is also developed between the umbilical wall and the inner lateral furrow. The umbilical wall is rather steep, but rounded. The phragmocone bears a longitudinal striation. The suture line is very complicate even in the premature stage.

Comparisons. – If the pre-mature "oppeliid" ribbing stage or the keel is preserved, *S. oppeliisculptum* n. sp. cannot be misidentified. The mature stage resembles some slender morphospecies of *Strigoceras*, like *S. symplectum* (Buckman), which might represent a phyletic forerunner. The oppeliid sculpture strongly resembles that of true *Oppelia*, like *O. pleurifer* (Buckman), but it is equally developed in *Granulochetoceras*.

Discussion and remarks. – At first sight it seems strange to place the roots of *Granulochetoceras* in *Strigoceras*. According to previously published data, *Granulochetoceras* is restricted to the Late Jurassic, ranging from the Planula Zone to the Beckeri Zone of the Kimmeridgian. The stratigraphically youngest known record of this genus is a specimen of *G. ornatum* (Berckhemer & Hölder) reported from the middle Ulmense Subzone of the Beckeri Zone (Schweigert 1998, pl. 3, fig. 4). However, typical specimens of *Granulochetoceras* are rare in the basal Athleta Zone of western France (oral communication of P.-Y. Baloge, Angers) and in eastern Switzerland (Fig. 26B, from the Herznach iron mine) thus bridging the absence of this lineage between the Bajocian and the basal Kimmeridgian. The taxon from the Late Callovian was first recorded and described from Villány (Hungary) by Lóczy (1915: 341, pl. 3, fig. 18) as "*Oppelia* (*Petitclercia* ?) *hungarica*", but not recognized as a *Granulochetoceras* until this study. A striation is developed only in some well preserved specimens of *Granulochetoceras*, like in the figured examples of *G. argonautoides* (Mayer) from the Lower Kimmeridgian (Divisum Zone) of eastern Swabia (Fig. 26C, D). To date this has not been recorded in previous literature. As in *Strigoceras*, the striation is only visible in specimens with preserved shell or in internal moulds on which the shell ornamentation is superimposed. The microconch partners of these forms are tentative. It is likely that the unique "?*Cymaceras* (?) sp." illustrated from the Upper Jurassic of northern Iran (Seyed-Emami et al. 1998, pl. 1, fig. 1) represents such a microconch partner. A Kimmeridgian offshoot of *Granulochetoceras*, the genus *Cymaceras* Quenstedt, 1887, also exhibits both a spiral striation and lateral spiral grooves (Kuhn 1933; Schairer & Schlampp 1991), thus indicating its affiliation to Strigoceratinae. In *Cymaceras* the corresponding microconchs are well-known and described as a separate genus or subgenus *Trochiskioceras* (Schairer & Schlampp 1991; Schick 2004).

The serration and undulation of the keel of *Granulochetoceras* also resembles that of *Phlycticeras*, but since most other features (lateral furrows, narrow umbilicus, and rounded umbilical edge) are never seen in early species of *Phlycticeras* this serration must be a convergence. However, in a closely related group and in the same beds as the new species *G. oppeliisculptum* the enigmatic genus *Diplesioceras* Buckman, 1920 is recorded which also exhibits an undulating keel. A detailed review study of the genus *Granulochetoceras* is in progress.

Measurements

	d	h	w	u	r/2	h/d	w/d	u/d
SMNS 65379 (holotype)	87.0	52.5	(~20)	4.0	~35	0.60	0.23	0.05
dito	65.5	40.0	16.0	3.0	35	0.61	0.24	0.05

7. Other taxa previously included in *Strigoceras*

Prior to the recent revision of the genus *Phlycticeras* Hyatt, 1900 (Schweigert & Dietze 1998), some early representatives of this genus have often been included in the striate genus *Strigoceras*, despite the significantly differing keel, their lack of

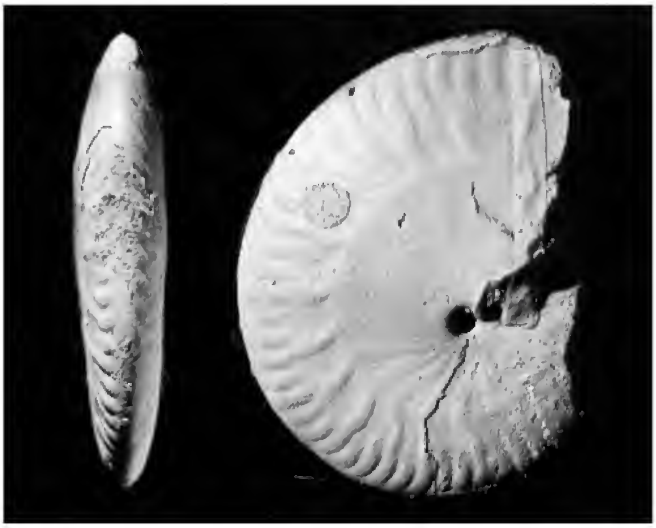

Fig. 27. *Hebetoxyites incongruens* Buckman, holotype, ventral and lateral views; Sandford Lane near Sherborne, S England; Inferior Oolite, Fossil Bed, *Brocchii* Bed of Buckman 1893, Lower Bajocian, Laeviuscula Zone; BGS GSM 47539. – ×1.

lateral furrows, and different dimorphic partners (*Oecoptychius* versus *Cadomoceras*).

Stringoceras pustuliferum introduced by Douvillé (1916) is a *Micromphalites*, an ammonite genus of still uncertain phyletic derivation but of assumed Arabian origin that exhibits a simplified suture line (Enay et al. 2001; Schlögl & Rakús 2004).

When erecting *Ammonites fissilobatus*, the type species of *Fissilobiceras* Buckman, Waagen (1867) suggested a close relation to *Ammonites truellei* d'Orbigny (see also Dorn 1935: 57). In his illustrated specimen, a striation is evident. This is due to a drawing technique and not present in the original specimen. Although the suture line of *Strigoceras* is almost as complex as in *Fissilobiceras*, the lateral lobes differ strongly in the two genera, and we interpreted *Fissilobiceras* as a late offshoot of hammatoceratids (see Dietze et al. 2005).

The monotypic *Kleistoxyites protrusus* Buckman, 1922, included either in *Strigoceras* by Imlay (1964) or in *Praestrigites* of Callomon & Chandler (1990), lacks both a striation and a septicarinate keel. The genus *Kleistoxyites* Buckman, 1922 must be excluded from Strigoceratidae. It is most likely an early representative of the *Oxycerites* lineage of Oppeliidae. The same must be said from the holotype of *Hebetoxyites clypeus* Buckman. This was erroneously assigned to *Strigoceras* by Sadki et al. (1986). *Hebetoxyites incongruens* Buckman, 1924 is another closely related form which strongly resembles *Strigoceras* in its ribbing style, but also totally lacking both keel and spiral striation (Fig. 27). The type species of *Hebetoxyites*, *H. hebes* Buckman, 1924, also lacks these features and surely does not belong to strigoceratids.

Liroxyites Imlay, 1961, is another genus homoeomorphic with *Strigoceras*. Originally described from the Bajocian of Alaska (Imlay 1961), *Liroxyites* lacks a septicarinate keel, a longitudinal striation, and any secondary ribbing. In contrast, it shows a somewhat eccentric coiling of the bodychamber. Nevertheless, this genus was treated as a subgenus of *Strigoceras* by SANDOVAL & WESTERMANN (1986). The specimens referred to this genus from Mexico by these authors, however, in fact represent true *Strigoceras* (see p. 25).

A strigoceratid ammonite from the Aalenian of Hungary figured by PRINZ (1904), re-figured by GÉCZY (1967, pl. 26, fig. 2) as *Praestrigites subaspidoides* (VACEK), is most probably correctly identified at specific level but belongs to *Csernyeiceras* (see SCHWEIGERT et al. 2000). This specimen differs from *Praestrigites* (or *Strigoceras*, respectively) in details of the suture line, a relatively wide umbilicus, and especially in the presence of a high and razor-sharp septicarinate keel.

BRASIL (1895) tentatively included *Ammonites mirabilis* GROSSOUVRE, 1891, the later type species of *Petitclercia* ROLLIER, 1909, in *Strigoceras*. Most probably *Petitclercia* represents an offshoot of Phlycticeratinae, in respect of its three longitudinal rows of nodules on the flanks reflecting homologous sculpture characters of the Early Callovian *Phlycticeras mexicanum* (SANDOVAL & WESTERMANN) (see SCHWEIGERT et al. 1999). The dimorphism in *Petitclercia* is still unclear. *Oppelia (Petitclercia ?) hungarica* LÓCZY, 1915 is reinterpreted here to be a Callovian chronospecies of *Granulochetoceras* (see p. 48).

8. *Cadomoceras*, the presumed microconch partner of *Strigoceras*

Following our previous studies on dimorphism in *Phlycticeras/Oecoptychius* (SCHWEIGERT & DIETZE 1998, 1999; SCHWEIGERT et al. 2003) we here follow the suggestion of STURANI (1971) who interpreted the microconchiate genus *Cadomoceras* as representing the partner of *Strigoceras*. In support of our arguments and those put forward by earlier authors (see STURANI 1971) we have observed a weak spiral striation in a few specimens of *Cadomoceras* where the shell is preserved. Collectors surely often overlooked the small and poorly sculptured shells of *Cadomoceras*; consequently the studied material is much less than that of the corresponding macroconchs. A preservational bias is also considered, e. g. by dissolution of small shells in the Tethyan Ammonitico Rosso lithology, whereas they are well represented in the coeval neptunian dykes (e.g., WENDT 1971), where early cementation processes prevented the fragile shells from dissolution.

Genus *Cadomoceras* MUNIER-CHALMAS, 1892 [m]

Type species: *Ammonites cadomensis* DEFRANCE in DE BLAINVILLE, 1840, by original designation of MUNIER-CHALMAS (1892).

Species included: *Ammonites cadomensis* DEFRANCE in DE BLAINVILLE, 1840; *Cadomoceras costellatum* BUCKMAN, 1923; *Cadomoceras carinatum* BUCKMAN, 1923; *Ammonites sullyense* BRASIL, 1895; *Cadomoceras nepos* PARONA, 1896. Synonymous taxa are excluded from this list.

Diagnosis. – Small microconch with eccentric bodychamber, large spatulate apophyses, ventral rostrum, shell smooth or occassionally with falcoid secondaries, venter carinate or rounded.

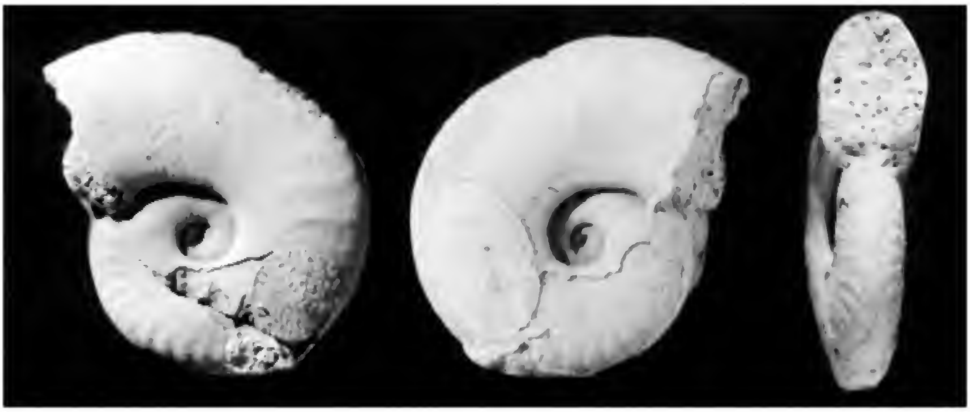

Fig. 28. *Cadomoceras costellatum* Buckman, holotype, lateral and ventral views; Sandford Lane near Sherborne, S England; Inferior Oolite, Fossil Bed, middle *Brocchii* Bed of Buckman 1893, Lower Bajocian, Laeviuscula Zone; BGS GSM 37307. – ×2.

Cadomoceras costellatum Buckman, 1923

Fig. 28

v *1923 *Cadomoceras costellatum*, nov. – Buckman, pl. 457.
? pars 1968 *Sonninia (Peocilomorphus) boweri minima* (Hiltermann). – Huf, pl. 4, fig. 6 only.
v 1971 *Cadomoceras carinatum* Buckman. – Wendt, pp. 156f.
1983 *Cadomoceras* cfr. *costellatum*. – Pavia, pl. 7, fig. 3.
1983 *Cadomoceras* sp. – Sandoval, p. 117.
1985 *Cadomoceras ellipticum* Buckman, 1923. – Fernández López, p. 147, pl. 13, fig. 7.
1985 *S. (Cadomoceras)* cf. *costellatum*. – Sandoval, pl. 1, figs. 11–12.
1986 *Cadomoceras costellatum*. – Sadki et al., tab.-fig. 4.
1986 *Cadomoceras* cf. *costellatum*. – Sandoval, p. 446.
v 1990 *Cadomoceras costellatum*. – Callomon & Chandler, p. 98.
pars 1994 *Cadomoceras*. – Sadki, tab.-fig. 3. – [1994a].
1994 *Cadomoceras costellatum*. – Sadki, tab.-fig. 4. – [1994a].
1996 *Cadomoceras*. – Sadki, p. 140, text-figs. 13, 46.

Holotype: Buckman (1923, pl. 457) BGS GSM 37307; re-figured herein as Fig. 28.

Type locality: Sandford Lane, Dorset, England.

Type horizon: Inferior Oolite, Sandford Lane Fossil Bed, "*Brocchi* Bed" (Early Bajocian, late Laeviuscula Zone).

Stratigraphic range: Discites Zone to Laeviuscula Zone; cf.-specimens were recorded from the Discites Zone and Ovale Zone of Spain and Morocco (Sandoval 1990: 145; Sadki 1994a: text-figs. 3–4, pl. 28; Sadki 1996, tab.-figs. 13, 46). The stratigraphically oldest unequivocal specimen is recorded from Sicily by Wendt (1971). It comes from an ammonite assemblage recovered from a neptunian dyke of early Discites Zone age, according to the co-occurrence of *Rhodaniceras prosphues* (Buckman), *Eudmetoceras* sp. and *Haplopleuroceras* sp. indicative of this level (cf. Sadki 1994a, fig. 2, 1994b, fig. 3).

Studied material: 7 specimens.

Records: England, Spain, Western Alps, Sicily, Morocco, ? NW Germany.

Diagnosis. – Small, almost unsculptured species of *Cadomoceras* with short carinate stage.

Description. – The holotype of *C. costellatum* is a complete specimen with the shell intact bearing large lappets at its aperture. The venter is carinate in the medium ontogenetic stage. In the last whorl, this keel fades out, and the venter becomes rounded. On the ventrolateral part of the flanks, a weak striation is developed in the holotype. Ribbing sculpture is usually lacking. The eccentric bodychamber is typical for the whole genus, and not restricted to this chronospecies only.

Remarks. – A small microconch ammonite from the Bajocian Laeviuscula Zone of NW Germany illustrated by Huf (1968, pl. 4, fig. 6) most probably represents a *Cadomoceras*. It differs from co-occurring microconch sonniniids by an eccentric bodychamber and the absence of a keel. The latter specimen, however, is extremely small and not representative for the average morphology of the chronospecies *C. costellatum*.

Measurements

	d	h	w	u	h/d	w/d	u/d
GSM 37307 (holotype)	23.2	11.0	6.8	4.5	0.47	0.29	0.19

Cadomoceras carinatum Buckman, 1923

Figs. 29–31

v *1923 *Cadomoceras carinatum*, nov. – Buckman, pl. 456.
v 1923 *Cadomoceras ellipticum*, nov. – Buckman, pl. 455, figs. 1–3.
v 1971 *Cadomoceras ellipticum* Buckman. – Wendt, p. 157.
v 1975 *Cadomoceras carinatum* Buckman. – Hinkelbein, p. 149, tab.-fig. 11.
1977 *Cadomoceras*. – Fernández López, p. 52.
1979 *Cadomoceras carinatum*. – Parsons, p. 148, table 4.
1979 *C. ellipticum*. – Parsons, p. 148, table 4.
1983 *Cadomoceras* sp. – Sandoval, tab.-fig. 77A.
1983 *Cadomoceras ellipticum*. – Pavia, pl. 7, fig. 7.
v 1984 *Dorsetensia* sp. – Dietl et al., p. 310, text-fig. 2.3.
1988 *Cadomoceras ellipticum* Buck. – Fernández López et al., p. 55.
1990 *Cadomoceras ellipticum*. – Sandoval, p. 148.
1996 *Cadomoceras ellipticum* Buckman. – Sadki, pp. 141, 183, text-fig. 46, pl. 5, fig. 9.
1996 *Cadomoceras carinatum* Buck. – Sadki, pp. 84, 142, tab.-fig. 46.
1996 *Cadomoceras costellatum*. – Sadki, tab.-fig. 14.
v 2006 *Cadomoceras* sp. – Chandler et al., tab.-fig. 2.

Holotype: Buckman (1923, pl. 456), BGS GSM 37306; re-figured here as Fig. 29.
Type locality: Dundry Hill, near Bristol, Avon, England.
Type horizon: Inferior Oolite, bed 10b of South Main Road Quarry (Bajocian, Sauzei Zone), see Parsons (1979: 148).
Stratigraphic range: Sauzei Zone.
Studied material: 10 specimens.
Records: England, Spain, Morocco, Southern Alps, Sicily, SW Germany, NW Germany (this study, Fig. 31D).

Diagnosis. – Small, weakly ribbed species of *Cadomoceras* with long-persisting carinate stage.

Description. – The holotype of *C. carinatum* Buckman is an almost complete adult specimen; only the lappets are partly broken. The second half of the bodychamber still has the shell on which in oblique view fine spiral striae are visible. Otherwise the shell is unsculptured. In the first half of the last whorl the venter is cari-

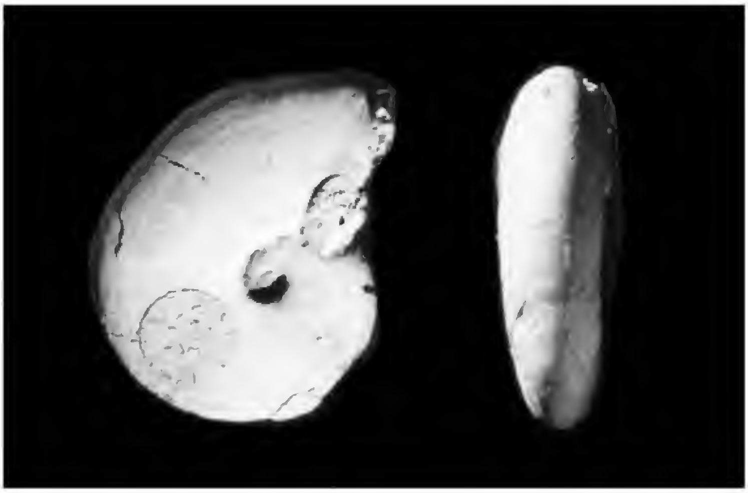

Fig. 29. *Cadomoceras carinatum* Buckman, holotype, lateral and ventral views; Dundry, Somerset, S England; Inferior Oolite, Ironshot Bed, Lower Bajocian, Sauzei Zone; BGS GSM 37306. – ×2.

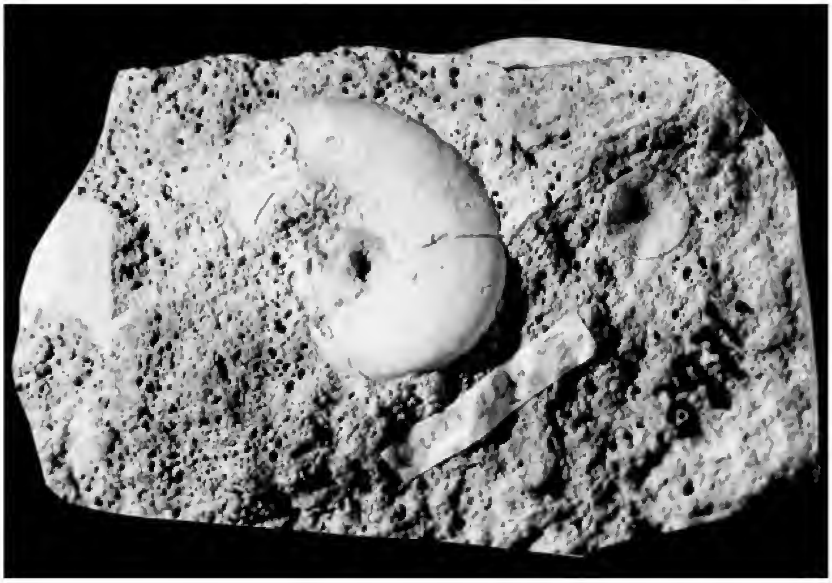

Fig. 30. *Cadomoceras carinatum* Buckman (= original specimen of *Cadomoceras ellipticum* Buckman, 1923, pl. 455, fig. 3), lateral view; Dundry, Somerset, S England; Inferior Oolite, Ironshot Bed, Lower Bajocian, Sauzei Zone; BGS GSM 37305. – ×2.

nate after which it becomes rounded. *C. ellipticum* Buckman (Fig. 30) does not differ significantly from *C. carinatum* Buckman and also exhibits the typical carinate venter. Both type specimens come from the same bed and horizon and must be regarded as conspecific. The date of erection of the two taxa was the same and we pre-

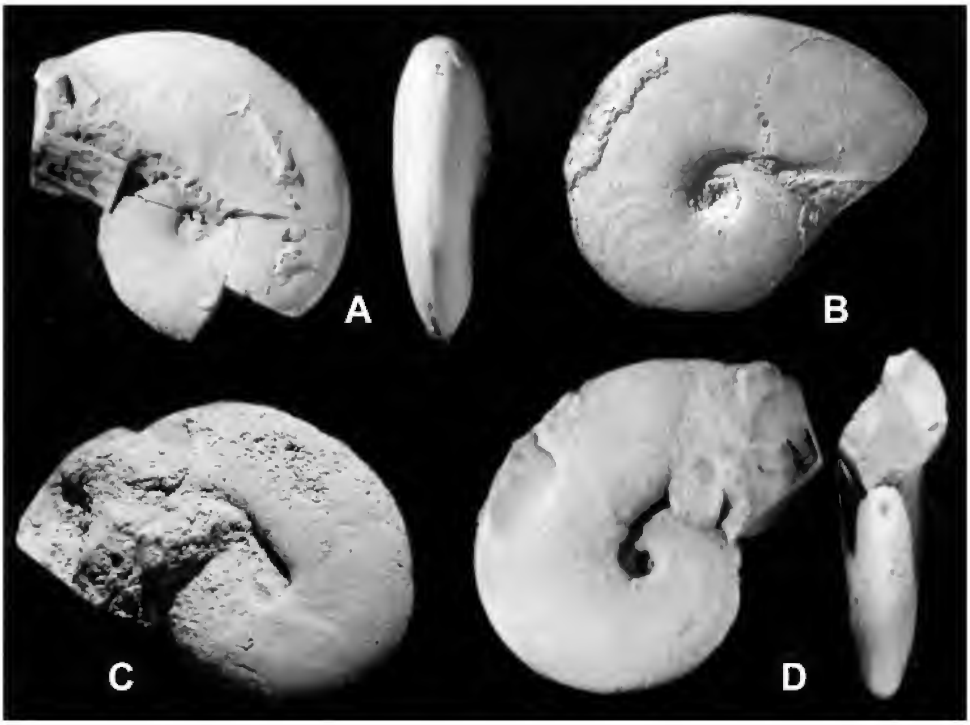

Fig. 31. *Cadomoceras carinatum* Buckman. **A.** Lateral and ventral views; Albarracín, Keltiberian Ranges, E Spain; bed 18d in section A of Hinkelbein (1975, fig. 11), Chelva Formation, Lower Bajocian, Sauzei Zone; SMNS 65384 (Coll. K. Hinkelbein). **B.** Lateral view; Sandford Lane near Sherborne, Dorset; Inferior Oolite, Lower Bajocian, bed 6b, Sauzei Zone (horizon Bj-11 of Callomon 1995); SMNS 67160 (ex coll. V. Dietze). **C.** Lateral view; Talheim am Lupfen, SW Germany; basal Humphriesioolith Formation, Lower Bajocian, Sauzei Zone; SMNS 65386 (leg. W. Ludwig). **D.** Lateral view; Gerzen, NW Germany; "Coronatenschichten" Formation (section see Huf 1968: 16), Lower Bajocian, Sauzei Zone, Pinguis-Subzone; IFGT 1905-2. – ×2.

fer here to use *C. carinatum* instead of *C. ellipticum* on grounds of preservation of the holotypes.

Comparisons. – *C. carinatum* differs from other chronospecies of the genus in its well-developed long persisting carinate stage of the adult bodychamber combined with weak ribbing sculpture.

Measurements

	d	h	w	u	h/d	w/d	u/d
GSM 37306 (holotype)	24.0	11.2	6.8	4.5	0.46	0.28	0.19
GSM 37305 (Fig. 30)	19.5	9.5	–	3.3	0.49	–	0.17
IFGT 1905-2 (Fig. 31D)	20.0	10.0	6.2	3.0	0.50	0.31	0.15
SMNS 65384 /Fig. 31A)	~24	10.0	6.1	3.0	0.41	0.25	0.12

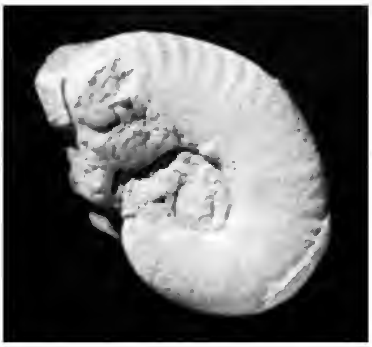

Fig. 32. *Cadomoceras sullyense* (Brasil), lateral and ventral views; Villel, Keltiberian Ranges, E Spain; bed 17 in section E of Hinkelbein (1975, fig. 12), Chelva Formation, Lower Bajocian, Humphriesianum Zone; SMNS 65387 (Coll. K. Hinkelbein). – ×2.

Cadomoceras sullyense (Brasil, 1895)
Fig. 32

* 1895 *Ammonites Sullyense* nov. sp. – Brasil, p. 41, pl. 4, figs. 8–9.
1918 *Cadomoceras sullyense* Brasil. – Coemme, p. 48, pl. 6, figs. 1–3.
1929 *Haploceras* sp. – Greppin & Tobler, p. 542.
1964 *Cadomoceras sullyense.* – Hölder, p. 90.
1964 *Cadomoceras sullyense.* – Rioult, p. 245.
1964 *Cadomoceras sullyense* Brasil. – Sturani, p. 26, pl. 4, fig. 7. – [1964b].
1964 *Cadomoceras nepos.* – Sturani, p. 25. – [1964b].
1964 *Cadomoceras cadomense.* – Sturani, p. 25. – [1964b].
1971 *Cadomoceras sullyense* Brasil. – Sturani, p. 122, pl. 5, figs. 1–5.
1971 *Cadomoceras* n. sp. aff. *sullyense.* – Sturani, p. 123, pl. 5, fig. 6.
1976 *S. (Cadomoceras) sullyense* Brasil. – Parsons, p. 126.
1976 *S. (Cadomoceras)* sp. – Parsons, pp. 126, 131.
v 1980 *Cadomoceras.* – Dietl & Rieber, p. 65.
1985 *Cadomoceras cadomense* (Defrance) 1846. – Fernández López, p. 140, pl. 13, fig. 6.
1985 *Cadomoceras sullyense* Brasil, 1893. – Fernández López, p. 142, pl. 13, fig. 7.
1989 *Cadomoceras.* – Alvaro et al., p. 82.
1993 *Cadomoceras cadomense.* – Elmi & Rulleau, p. 155.
pars 1994 *Cadomoceras* sp. – Fernández López & Mouterde, p. 122. – [1994a].
v 1995 *Strigoceras (Cadomoceras) sullyense* Brasil. – Ohmert et al., p. 73, pl. 4, fig. 5.
pars 1996 *Cadomoceras* sp. – Sadki, tab.-fig. 46.
v 1999 *Cadomoceras sullyense.* – Schweigert & Dietze, p. 54.
v 2000 *Cadomoceras sullyense* (Brasil). – Huxtable, p. 105.
v 2006 *Strigoceras (Cadomoceras) sulleyensis* (Brazil). – Huxtable, p. 82.

Lectotype: Specimen figured by Brasil (1895, pl. 6, fig. 8) probably in the collections of the University of Caen, France.

Type locality: Sully, Normandy.

Type horizon: Oolithe Ferrugineuse de Bayeux (Bajocian, Humphriesianum Zone, probably Romani Subzone, horizon à *Dorsetensia edouardiana*).

Stratigraphic range: Humphriesianum Zone.

Studied material: 15 specimens.

Records: France, Spain, Morocco, England, SW Germany, Southern Alps.

Diagnosis. – Poorly sculptured species of *Cadomoceras* with rounded venter in the adult stage.

Description. – See Brasil (1895: 41). The lectotype of *C. sullyense* (Brasil) is a complete specimen intact with shell and well-developed lappets. The shell is almost smooth. Ventrally, a keel is developed only in the inner whorls, sometimes persisting to the first half of the outer whorl. In the eccentric bodychamber, the venter becomes rounded.

Comparisons. – Compared with other chronospecies of *Cadomoceras*, *C. sullyense* is rather slender and lacking any significant sculpture. The carinate stage may persist to the first half of the bodychamber, thus fading earlier than in the preceding *C. carinatum* Buckman.

Measurements

	d	h	w	u	h/d	w/d	u/d
Lectotype (after photograph)	14.5	6.5	3.0	~4	0.45	0.21	0.27
SMNS 65386	18.7	8.5	5.3	2.0	0.45	0.28	0.11

Cadomoceras nepos Parona, 1896

Figs. 16G–I, 33–34

*1896 *Cadomoceras nepos* n. f. – Parona, p. 15, pl. 1, fig. 13.

1896 *Oecotraustes minor* n. f. – Parona, p. 15, pl. 1, fig. 12.

1918 *Cadomoceras cadomense* var. *acostatum* nob. – Coemme, p. 47. – [objective synonym of *C. nepos*]

v 1920 *Cadomoceras costatum*, nov. – Buckman, pl. 189.

v 1923 *Cadomoceras simulacrum*, nov. – Buckman, pl. 458 [Fig. 33A].

1962 *Oecotraustes* nov. sp. – Sato, p. 69, pl. 3, fig. 7.

1971 *Cadomoceras nepos* Parona. – Sturani, p. 123, pl. 5, fig. 7 (= refiguration of lectotype), figs. 8–10.

1971 *Cadomoceras* cf. *cadomense* (Defr.). – Sturani, p. 125, pl. 5, fig. 11.

1971 *Cadomoceras cadomense* (Defr.). – Sturani, p. 125, pl. 5, figs. 12–15.

v 1971 *Cadomoceras* sp. – Wendt, p. 158.

v 1975 *Cadomoceras cadomense* (Blainville). – Hinkelbein, p. 155, tab.-figs. 11–12.

1976 *Cadomoceras simulacrum*. – Parsons, p. 120, table 2.

1976 *S. (Cadomoceras) sullyense*. – Parsons, pp. 126, 129–130.

1976 *S. (Cadomoceras) nepos*. – Parsons, pp. 126, 129–130.

1979 *Cadomoceras nepos* Parona. – Linares & Sandoval, p. 286, tab.-fig. 2, pl. 2, fig. 6.

1979 *Cadomoceras cadomense* (Defrance). – Linares & Sandoval, p. 287, pl. 2, fig. 7.

1983 *Cadomoceras* sp. – Sandoval, p. 122, tab.-fig. 77A.

1983 *C. nepos* (Parona). – Sandoval, p. 122, tab.-fig. 77A.

1983 *C. cadomense* (Defrance). – Sandoval, p. 122, tab.-fig. 77A.

1985 *Cadomoceras nepos* Parona, 1896. – Fernández López, p. 143, pl. 13, fig. 9.

1985 *Cadomoceras minor* (Parona), 1896. – Fernández López, p. 145, pl. 13, fig. 10.

1985 *S. (Cadomoceras) nepos* (Trauth, 1922). – Sandoval, p. 104, pl. 1, figs. 13–14, pl. 2, figs. 1–2.

1990 *Cadomoceras cadomense* (Defrance). – Sandoval, p. 151.

1990 *Cadomoceras nepos* Parona. – Sandoval, p. 151, pl. 3, fig. 6.

v 1993 *Cadomoceras cadomense*. – Besnosov & Mitta, p. 26, pl. 1, figs. 8–9.

v 1998 *Strigoceras (Cadomoceras) cadomense*. – Besnosov & Mitta, pl. 8, fig. 1.

v 2000 *Strigoceras (Cadomoceras) cadomense* (Defrance, 1840). – Besnosov & Mitta, pp. 13, 51, pl. 1, figs. 7–8.

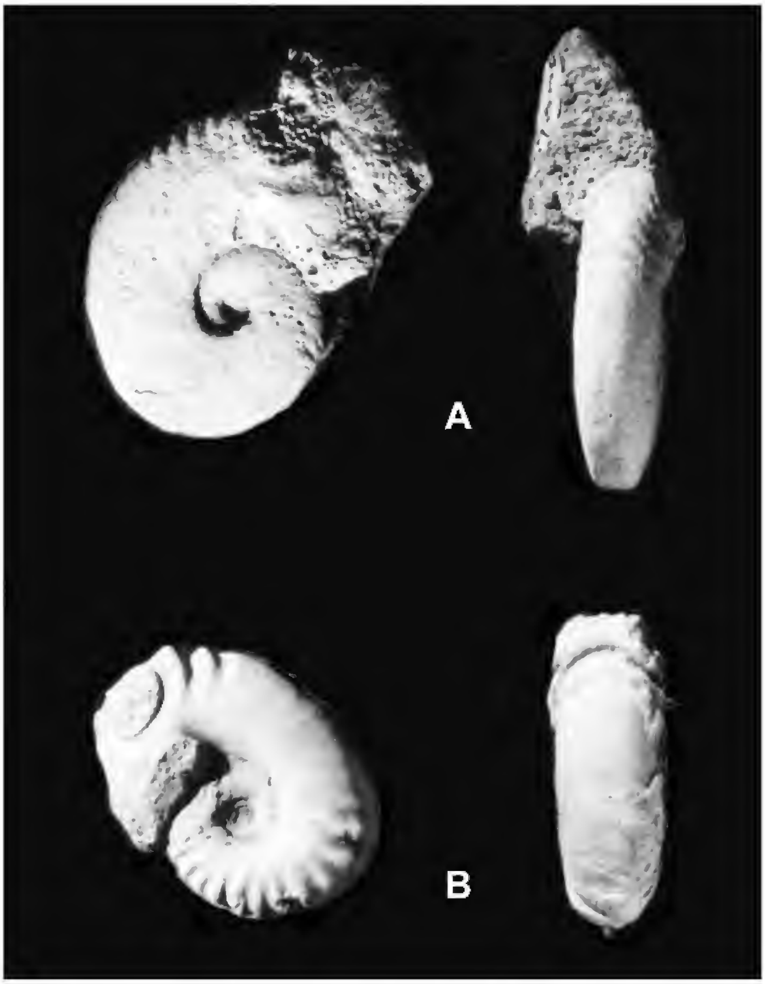

Fig. 33. A. *Cadomoceras nepos* PARONA (= holotype of *Cadomoceras simulacrum* BUCKMAN), lateral and ventral views; Sherborne, “Combe”, S England; Inferior Oolite, Upper Bajocian, Niortense Zone; BGS GSM 37308. **B.** *Cadomoceras nepos* PARONA var. *costatum* BUCKMAN (=holotype of *Cadomoceras costatum* BUCKMAN),lateral and ventral views; Burton Bradstock, Dorset, S England; Inferior Oolite, White Bed, Upper Bajocian, Niortense Zone; BGS GSM 47105. – ×2.

Lectotype: Designated by STURANI (1971, pl. 5, fig. 7) from the PARONA collection, collection of the Museo di Geologia e Paleontologia of the University of Padova, Italy.

Type locality: Monte Meletta near Gallio, Altopiano di Asiago, Southern Alps, Italy.

Type horizon: Lumachella à *Posidonia alpina* Beds (Bajocian, Niortense Zone).

As type horizon of the conspecific *C. simulacrum* BUCKMAN, PARSONS (1976) indicated bed 6d of Frogden quarry, Oborne, Dorset, the age of which is Baculata Subzone of Niortense Zone.

Stratigraphic range: Niortense Zone.

Studied material: Ca. 20 specimens.

Records: England, France, Spain, Southern Alps, Sicily, Caucasus, Turkmenistan, Dagestan, Japan.

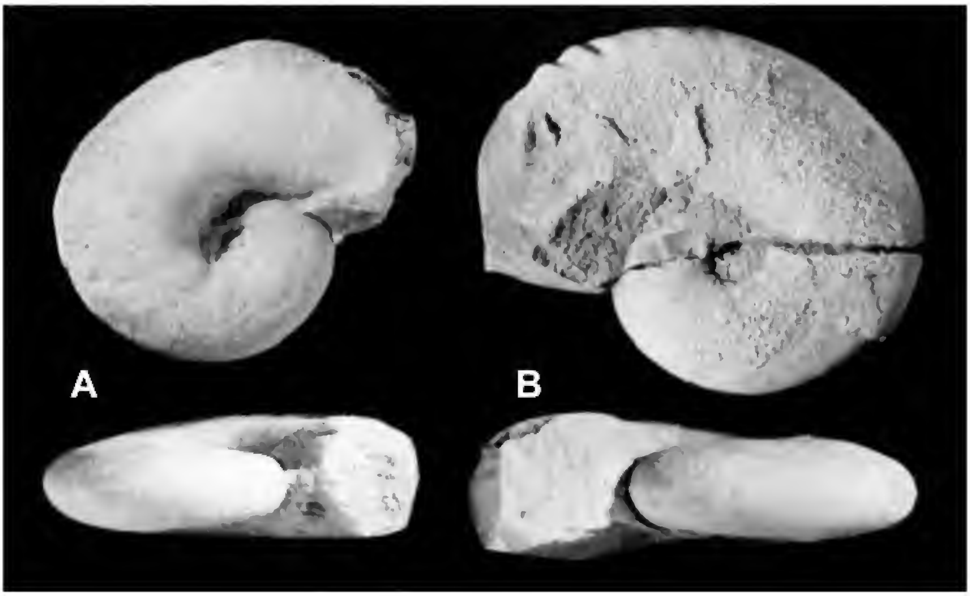

Fig. 34. A–B. *Cadomoceras nepos* Parona, lateral and ventral views; Albarracín, Keltiberian Ranges, E Spain; bed 30 l in section A of Hinkelbein (1975, fig. 11), Chelva Formation, Upper Bajocian, Niortense Zone, Baculata Subzone; SMNS 65383/1–2 (Coll. K. Hinkelbein). – ×2.

Diagnosis. – Medium-size species of *Cadomoceras* with a stage showing strong ventrolateral ribbing just behind the aperture.

Description. – See Sturani (1971). In *C. nepos* ventrolateral ribbing is usually developed just behind the lappeted aperture and also in the first half of the last whorl which shows a strongly eccentric coiling. Within the variation of this chronospecies, some extremely broad and coarse-ribbed specimens occur (*C.* "*costatum*" Buckman), corresponding to similar macroconch specimens. The taxon *costatum* introduced by Buckman (1923) is therefore treated here as a variety of *C. nepos* (Fig. 33B).

Comparisons. – *C. nepos* is characterized by a long persistent smooth stage of the adult bodychamber followed by scarce ribbing behind the aperture. There are transitions between *C. nepos* and the younger *C. cadomense*. In the latter species the genus reaches its largest widths.

Measurements

	d	h	w	u	h/d	w/d	u/d
Lectotype	19.2	8.4	5.6	4.8	0.44	0.29	0.25
GSM 47105 (Fig. 33B)	19.5	8.0	7.3	6.3	0.41	0.37	0.32
SMNS 65383/1 (Fig. 34A)	20.0	9.3	7.6	5.7	0.46	0.38	0.29
GSM 37308 (Fig. 33A)	21.3	8.5	5.2	4.5	0.40	0.24	0.21
SMNS 65383/2 (Fig. 34B)	24.5	12.0	8.5	5.8	0.49	0.35	0.24

Cadomoceras cadomense (Defrance in de Blainville, 1840)

Fig.35

1830 [Ammonite de Caen]. – Defrance, pl. (2)18, fig. 1.
*1840 *Ammonites cadomensis*. – de Blainville, p. 153.
1845 *Ammonites cadomensis*. – d'Orbigny, pl. 129, figs. 4–6.
1909 *Ammonites cadomensis* Defrance. – Douvillé, pl. 134, fig. C1.
1918 *Cadomoceras cadomense* Defrance. – Coemme, p. 44, pl. 6, figs. 4–8.
1938 *Cadomoceras cadomense* Defr. – Roman, pl. 16, fig. 166.
1951 *Cadomoceras cadomense*. – Arkell, p. 49.
1957 *Cadomoceras cadomense* (Defrance in de Blainville). – Arkell, p. L 273, fig. 315.6.
cf. 1963 *Oecotraustes nodifer* Buckman. – Krymholtz & Stankevitch, p. 113, pl. 1, fig. 8.
1964 *Cadomoceras cadomense*. – Hölder, pp. 90–91.
1968 *Cadomoceras cadomense*. – Pavia & Sturani, p. 314.
1973 *Cadomoceras* cfr. *cadomense*. – Pavia, table 3.
1975 *Cadomoceras cadomense*. – Parsons, p. 9.
1982 *Cadomoceras nepos* Parona. – Fernández López, tab.-fig. 2, pl. 1, fig. 5.
1982 *Cadomoceras cadomense*. – Fernández López, tab.-fig. 2.
1988 *Cadomoceras nepos* Parona. – Fernández López, p. 77.
1988 *Cadomoceras* sp. – Fernández López & Aurell, tab.-fig. 4.
v 1990 *Cadomoceras* sp. – Dietze & Stolmar, p. 167 top.
1994 *Cadomoceras cadomense* (Blainville, 1840). – Rioult in Fischer, p. 114, pl. 50, figs. 3 (= reproduction of the lectotype)–4.
1995 *Cadomoceras* cf. *costatum*. – Gauthier et al., p. 322.
1997 *Cadomoceras cadomense*. – Rioult et al., p. 52.
1997 *Cadomoceras cadomense*. – Fernández López et al., tab.-fig. 12.
1997 *Cadomoceras nepos*. – Fernández López et al., tab.-fig. 12.
1998 *Cadomoceras cadomense*. – Fernández López et al., tab.-fig. 11.
1998 *Cadomoceras nepos*. – Fernández López et al., tab.-fig. 11.

Lectotype: Specimen from the E. Deslongchamps collection, photograph in Douvillé (1909, pl. 134, fig. C1), see Arkell (1951: 49); according to Rioult (in Fischer 1994) destroyed in 1944 during World War II.

Type locality: Bayeux, Calvados, France.

Type horizon: Oolithe ferrugineuse de Bayeux (Late Bajocian, Parkinsoni Zone, probably Truellei Subzone).

Stratigraphic range: Garantiana Zone to Zigzag Zone, Convergens Subzone.

Studied material: 5 specimens.

Records: France, England, Spain, Southern and Western Alps, Dagestan.

Diagnosis. – *Cadomoceras* with relatively stout shell and ventrolateral ribbing occurring at the beginning of the last whorl, and again behind the aperture, with a plain unsculptured region inbetween.

Description. – See Rioult (in Fischer 1994: 114). Because the lectotype of *C. cadomense* is destroyed, a better description of this taxon may be obtained from topotypes, e.g. the specimen figured by Rioult (in Fischer 1994, pl. 50, fig. 4). Usually, the ventrolateral ribbing appears at the beginning of the last whorl, then almost fades out, reappearing for a short distance in the bend of the bodychamber. Sparse ribs are often present just behind the lappeted aperture as in the older chronospecies *C. nepos* Parona. The venter on the last whorl is rounded. In general, the whorl widths of *C. cadomense* are the biggest of the genus.

Comparisons. – *C. cadomense* is very close to *C. nepos*, but has stronger ribbing in the bend of the bodychamber. It commonly has a broader cross section, the broadest in the genus.

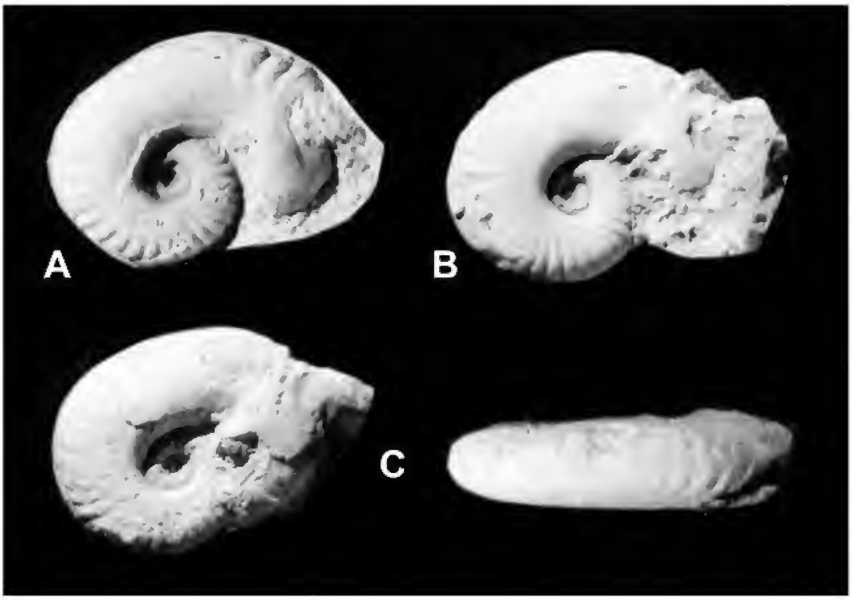

Fig. 35. *Cadomoceras cadomense* (DEFRANCE in DE BLAINVILLE). **A.** Lateral view; Burton Bradstock, Dorset, beach exposure; Inferior Oolite, Truellei Bed (bed 13 b of CALLOMON & CHANDLER 1994), Upper Bajocian, Parkinsoni Zone, Truellei Subzone, *Parkinsonia parkinsoni* β horizon; SMNS 65382 (leg. G. ERMER). **B.** Lateral view; Port-en-Bessin, France; Oolithe ferrugineuse de Bayeux, Upper Bajocian, Parkinsoni Zone, probably Acris Subzone; SMNS 67161 (ex coll. V. DIETZE). **C.** Lateral and ventral views; Burton Bradstock, Dorset, beach exposure; Inferior Oolite, Truellei Bed (bed 13 b of CALLOMON & CHANDLER 1994), Upper Bajocian, Parkinsoni Zone, Truellei Subzone, *Parkinsonia parkinsoni* β horizon; SMNS 67162 (ex coll. V. DIETZE). – ×2.

Measurements

	d	h	w	u	h/d	w/d	u/d
D'ORBIGNY specimen MNHM B. 46072	22.0	11.0	8.0	10.0	0.50	0.36	0.45
SMNS 67162 (Fig. 35C)	16.5	6.5	6.3	4.5	0.39	0.38	0.27
SMNS 65382 (Fig. 35A)	17.2	7.5	–	4.5	0.44	–	0.26

9. Phyletic history of *Strigoceras/Cadomoceras*

The microconch ammonites included in *Cadomoceras* strongly resemble the late Early Jurassic genus *Onychoceras* WUNSTORF, 1907, which extends up to the early Middle Jurassic (SCHWEIGERT et al. 2000). They are either smooth or widely-spaced ribbed forms, in contrast to more finely ribbed and thicker *Oecoptychius*. In both dimorphic partners *Phlycticeras/Oecoptychius* and *Strigoceras/Cadomoceras* the size ratio between macroconchs and microconchs is enormous, as much as 10–15 : 1. The same can be true for their presumed ancestors. *Phlycticeras* is phyletically linked with the Middle Jurassic genus *Csernyeiceras* GÉCZY, 1966, and its late Early Jurassic relative *Esericeras* BUCKMAN, 1920, and *Phlyseogrammoceras* BUCKMAN, 1901, as already discussed by SCHWEIGERT et al. (2000). Cladistic analysis by MOYNE & NEIGE (2004) identified strigoceratids ('*Praestrigites*'), early oppeliids s. str. *(Brad-*

fordia) and *Csernyeiceras* as closely allied, but lumped them together into a hammatoceratid ancestry. Strigoceratinae must have split from their Phlycticeratinae ancestors in the earliest Middle Jurassic. The diagnostic features for separation of *Strigoceras* from Phlycticeratinae are a very narrow umbilicus, a rounded umbilical wall, absence of umbilical or lateral nodules, and a low, smooth floored keel instead of a razor-sharp keel. Such features are fully developed in the earliest chronospecies known so far, *Strigoceras praenuntium* from the Middle Aalenian (see p. 9). More data than presently available are required for a better understanding of the earliest phyletic history of *Strigoceras*.

The dimorphic pair *Strigoceras/Cadomoceras* persists into the Early Bathonian, where to date *S. callomoni* n. sp. represents its youngest member. The most reliable records published prior to this study come from the Betic Cordilleras of southern Spain (SANDOVAL 1983: 123, text-fig. 77A) and from the Catalan Basin of southeastern Spain (FERNÁNDEZ LÓPEZ 2000). A Bathonian age for *Strigoceras kuznetsovi* KRYMHOLTZ & STANKEVITCH, 1963, from Dagestan was questioned by STURANI (1971: 125). The ammonite assemblage containing *Strigoceras kuznetsovi* also yields *Pseudocosmoceras michalskii* (BORISSJAK), and was tentatively correlated with the Convergens Subzone of the Early Bathonian (BESNOSOV & MITTA 1993: 15). The Early Bathonian age of *Pseudocosmoceras michalskii* (BORISSJAK) is still unconfirmed. New examples of endemic *P. michalskii* occuring with *S. kuznetsovi* make a Late Bajocian age for the assemblage more likely (MITTA 2004).

Another *Strigoceras* specimen said to come from the Upper Bathonian of Lechstedt near Hildesheim, northwestern Germany (WESTERMANN 1958: 54, pl. 17, fig. 6), most likely comes from a much older stratigraphical level at another Middle Jurassic locality in northwestern Germany; the clay-pit of Gerzen, where claystones of the Lower Bajocian were quarried. This specimen is preserved as a pyritic mould with aragonitic remains of the shell, therefore reworking of the specimen can be excluded. The slender cross section and ribbing sculpture of this specimen better related to a *Strigoceras* chronospecies of the Sauzei/Humphriesianum zones. From the (?)Sauzei Zone of Gerzen a corresponding *Cadomoceras carinatum* BUCKMAN is recorded and illustrated herein for the first time (Fig.31D). Similarly KUMM (1952) mentioned *Strigoceras truellei* from the latest Bajocian and from the Bathonian. He did not illustrate this material, and most likely the specimens represent either *Phlycticeras*, or the proposed finding levels were erroneous.

KRYSTYN (1971, 1972) reported a single specimen of *Strigoceras truellei* from an ammonite bed containing a Middle to Late Bathonian fauna. This specimen was interpreted as derived. Other "*Strigoceras* sp." were recorded from the Late Bathonian Retrocostatum Zone of Monte Kumeta, W Sicily, but not illustrated (DI STEFANO et al. 2002: 289). Photographs of the two specimens provided by courtesy of A. GALÁCZ (Budapest) allow them to be identified as nuclei and placed in *Phlycticeras* sp.

Our present knowledge records the extinction of *Strigoceras/Cadomoceras* in the Zigzag Zone, the youngest known record coming from the Macrescens Subzone (see above; Table 1). From this time onwards, the dimorphic pair *Phlycticeras/Oecoptychius* becomes significantly more abundant suggesting that it replaced *Strigoceras/Cadomoceras* ecologically.

10. Conclusions

The dimorphic couple *Strigoceras/Cadomoceras* forms a remarkably conservative lineage within Haploceratoidea, ranging from the Middle Aalenian to the Early Bathonian. The separation of Strigoceratinae and Phlycticeratinae from a common ancestor must have occurred at least in the Early Aalenian. *Strigoceras* is widely distributed in the western Tethys and adjacent areas, but absent in the Boreal Realm. In contrast to Phlycticeratinae it is also absent in the southern Pacific.

Within an isochronous population, macroconchs of Strigoceratinae show a wide variation in ontogeny, with specimens attaining adult characters at small diameters alongside others that reach gigantic size. In small individuals the suture line is remarkably more complex than in the contemporary large examples at equal diameters. In addition the development of the sculpture appears accelerated in small specimens. A trend observed in *Strigoceras* is the shifting of the centre of morphological variation during phylogeny leading to stouter morphs. Later in the Middle Jurassic a similar trend is observed in the *Phlycticeras* lineage of Strigoceratidae (cf. Schweigert & Dietze 1998). The reasons for these evolutionary trends are unknown.

The only direct descendant we included in Strigoceratinae is *Granulochetoceras* Geyer, 1960, which is linked with *Strigoceras* by a transitional form described here as *Granulochetoceras oppeliisculptum* n. sp. Another early species of *Granulochetoceras* is *G. hungaricum* (Lóczy, 1915) (see p. 48), recorded as an extreme rarity from the Late Callovian of France, Hungary, and Switzerland. Thus, the recorded stratigraphical range of *Granulochetoceras* extends now from the Late Bajocian to the Late Kimmeridgian.

In accordance with our data and previous studies, the following haploceratoid genera are included in Strigoceratinae: *Strigoceras* Quenstedt, 1886 [M], *Cadomoceras* Buckman, 1923 [m], *Granulochetoceras* Geyer, 1960 [M], *Cymaceras* Quenstedt, 1887 [M], and *Trochiskioceras* Schairer & Schlampp, 1991 [m].

The following genera are now included in Phlycticeratinae: *Phlycticeras* Hyatt, 1900 [M], *Oecoptychius* Neumayr, 1878 [m], *Csernyeiceras* Géczy, 1966 [M], *Phlyseogrammoceras* Buckman, 1901 [M], *Esericeras* Buckman, 1920 [M], *Onychoceras* Wunstorf, 1907 [m], *Strungia* Arkell, 1952 [M], *Petitclercia* Rollier, 1909 [M], *Oxydiscites* Dacqué, 1934 [M], and *Sphaerodomites* Rollier, 1909 [m].

Diplesioceras Buckman, 1920 and *Vastites* Arkell, 1951, are very rare and still poorly understood genera. They may also belong to Strigoceratidae but more material will be needed for further discussion.

11. References

Alvaro, M., Barnolas, A., Cabra, P., Comas-Rengifo, M. F., Fernández López, S. R., Goy, A., Del Olmo, P., Ramírez de Pozo, J., Simo, A. & Ureta, S. (1989): El Jurásico de Mallorca (Islas Baleares). – Cuadernos de Geología Ibérica, **13**: 67–120.

Arkell, W. J. (1933): The Jurassic System in Great Britain. XII + 681 pp.; Oxford (Clarendon Press).

Arkell, W. J. (1950): Classification of the Jurassic ammonites. – Journal of Paleontology, **24**: 354–364.

Arkell, W. J. (1951–1958): A monograph of English Bathonian Ammonites. – Monographs of the Palaeontological Society, 264 pp.; London.

Arkell, W. J. (1952): Jurassic ammonites from Jebel Tuwaiq, Central Arabia. – Philosophical Transactions of the Royal Society of London, Series B, **236**: 241–313.

Arkell, W. J. (1956): Jurassic Geology of the World. XV + 757 pp.; Edinburgh & London (Oliver & Boyd).

Arkell, W. J. (1957): Cephalopoda, Ammonoidea. – In: Moore, R. C. (ed.): Treatise on Invertebrate Palaeontology, Part L, Mollusca, **4**: L80–L490; Lawrence (University of Kansas Press).

Arp, G. (2001): Fazies, Stratigraphie und Ammonitenfauna des Mittleren und Oberen Dogger bei Neumarkt i. d. Opf. (Bajocium–Oxfordium, Süddeutschland). – Berliner geowissenschaftliche Abhandlungen, Reihe E, **36**: 189–241.

Atrops, F. (1974): Le Bajocien inférieur et moyen des Beni Bahdel au sud-ouest de Tlemcen (ouest Algérien). – Géologie méditerranéenne, **1** (2): 75–88.

Baldanza, A., Cresta, S. & Mattioli, E. (1990): Bajocian calcareous nannofossils from Monte Nerone area (Umbro-Marchean Apennine, Italy). – Memorie descrittive della Carta geologica d'Italia, **40**: 225–236.

Bayle, E. (1878): Fossiles principaux des terrains. Explication de la carte géologique de France, **4**: Atlas with 158 pls.; Paris.

Benetti, A. (1977): Note biostratigrafiche al Giurassico del "Covolo di Camposilvano" nei Monti Lessini Veronesi. – Studi Trentini di Scienzia naturale, **54**: 227–245.

Benhamou, M. & Elmi, S. (1994): Le Bajocien du massif culminant de L'Ouarsensis (Algerie). – Miscellanea del Servizio Geologico Nazionale, **5**: 271–275.

Besnosov, N. V. & Mitta, V. V. (1993): Late Bajocian and Bathonian ammonitids of the Northern Caucasus and Middle Asia. 348 pp.; Moskva (VNIGNI). – [In Russian]

Besnosov, N. V. & Mitta, V. V. (1998): Catalogue of Ammonitida and key sections of the Upper Bajocian – Lower Bathonian of North Caucasus. – Bulletin of CF VNIGNI, **1**: 1–70. – [In Russian]

Besnosov, N. V. & Mitta, V. V. (2000): Jurassic geology and ammonites of Great Balkhan (Western Turkmenistan). – Bulletin of CF VNIGNI, **5**: 1–115. – [In Russian]

Bircher, W. (1935): Studien im oberen Bajocien der Ostschweiz (Glarner- und St. Galleralpen). – Thesis at the University of Zurich, Switzerland. 179 pp.; Kairo (edited by the author).

Blainville, M. H. D. de (1840): Dictionnaire des Sciences Naturelles, supplément 1; Paris & Strasbourg (Levrault).

Brasil, L. (1895): Céphalopodes nouveaux ou peu connus des étages jurassiques de Normandie. – Bulletin de la Societé géologique du Normandie, **16**: 27–46.

Buckman, S. S. (1887–1907): Monograph of the ammonites of the Inferior Oolite Series. – Monographs of the Palaeonotological Society, CCLXII + 456 pp.; London.

Buckman, S. S. (1893): The Bajocian of the Sherborne district: its relation to subjacent and superjacent strata. – The Quarterly Journal of the Geological Society of London, **49**: 479–522.

Buckman, S. S. (1909–1930): Yorkshire type ammonites/Type ammonites, **1–7**: 790 pls.; London (Wheldon & Wesley/Wesley).

Buckman, S. S. (1910): Certain Jurassic (Lias – Oolite) strata of South Dorset; and their correlation. – The Quarterly Journal of the Geological Society of London, **66**: 52–89.

Buckman, S. S. & Wilson, E. (1896): Dundry Hill: its upper portion, or the beds marked as Inferior Oolite (g 5) in the maps of the Geological Survey. – The Quarterly Journal of the Geological Society of London, **52**: 665–720.

Callomon, J. H. (1963): Sexual dimorphism in Jurassic ammonites. – Transactions of the Leicester Literary and Philosophical Society, **57**: 21–56.

Callomon, J. H. (1995): Time from fossils: S. S. Buckman and Jurassic high-resolution geochronology. – In: Le Bas, M. J. (ed.): Milestones in Geology. – Memoirs of the Geological Society of London, **16**: 127–150.

Callomon, J. H. & Chandler, R. B. (1990): A review of the ammonite horizons of the Aalenian – Lower Bajocian Stages in the Middle Jurassic of southern England. – Memorie descrittive della Carta geologica d'Italia, **40**: 85–112.

Callomon, J. H. & Chandler, R. B. (1994): Some early Middle Jurassic ammonites of Tethyan affinities from the Aalenian of southern England. – Palaeopelagos, special publications, **1**: 17–40.

CALLOMON, J. H. & COPE, J. C. W. (1995): The Jurassic geology of Dorset. – In: TAYLOR, P. D. (ed.): Field geology of the British Jurassic: 51–103; Bath (Geological Society).

CALLOMON, J. H., DONOVAN, D. T. & HOWARTH, M. K. (2004a): F. A. QUENSTEDT's trinominal nomenclature (1845–1888): a proposal to stabilize the usage of the third names of ammonites and to place 34 important QUENSTEDT names of ammonites on the Official List of Specific Names in Zoology (Cephalopoda, Ammonoidea). – Bulletin of Zoological Nomenclature, **61**: 11–18.

CALLOMON, J. H., DONOVAN, D. T. & HOWARTH, M. K. (2004b): F. A. QUENSTEDT's trinominal nomenclature of Jurassic ammonites. – Palaeontology, **47**: 1063–1073.

CECCA, F., CRESTA, S., PALLINI, G. & SANTANTONIO, M. (1991): Il Giurassico Umbro-Marchigiano: Progressi nel periodo 1982–1991 sulla paleontologia e biostratigrafia ad ammoniti. Riflessi sull'inquadramento degli eventi sedimentari. – Palaeopelagos, **1**: 83–112.

CHANDLER, R. B., CALLOMON, J. H., KING, A., JEFFREYS, K., VARAH, M. & BENTLEY, A. (2006): The stratigraphy of the Inferior Oolite at South Main Road Quarry, Dundry, Avon. – Proceedings of the Geologists' Association, **117**: 345–375.

CHANDLER, R. B. & DIETZE, V. (2001): Sherborne und der Inferior Oolite. – In: WEIDERT, W. K. (ed.): Klassische Fundstellen der Paläontologie, **4**: 111–118; Korb (Goldschneck).

CHANDLER, R. B. & DIETZE, V. (2003): Burton Bradstock. – In: Coast and Country. Geology Walks in and around Dorset (including excursions within the World Heritage Site): 34–43; Dorchester (Dorset Geologists' Association Group).

COEMME, S. (1918): Note critique sur le genre *Cadomoceras*. – Bulletin de la Societé géologique de France, série 4, **17**: 44–54.

COX, B. M. & SUMBLER, M. G. (2002): British Jurassic Stratigraphy. – Geological Conservation Review Series, **26**: 508 pp.

CRESTA, S. (1988): Associations d'ammonites et biostratigraphie de l'Aalenien et du Bajocien inférieur des Apennins d'Ombrie-Marches (Italie Centrale). – In: ROCHA, R. B. & SOARES, R. F. (eds.): 2nd International Symposium on Jurassic Stratigraphy, Lisboa: 209–224; Lisboa.

CRESTA, S. & GALÁCZ, A. (1990): Mediterranean basal Bajocian ammonite faunas. Examples from Hungary and Italy. – Memorie descrittive della Carta geologica d'Italia, **40**: 165–198.

DACQUÉ, E. (1934): Wirbellose des Jura. – In: GÜRICH, G. (ed.): Leitfossilien, **7/2**: 273–582; Berlin (Borntraeger).

DEFRANCE, M. (1830): Dictionnaire des Sciences Naturelle: planches Zoologie, Conchyliologie et Malacologie. Pls. 17–18; Paris & Strasbourg (Levrault).

DELLA BRUNA, G. & MARTIRE, L. (1985): La successione giurassica (Pliensbachiano – Kimmeridgiano) delle Alpi Feltrine (Belluno). – Rivista Italiana di Paleontologia e Stratigrafia, **91**: 15–62.

DIETL, G. (1974): Zur Stratigraphie und Ammonitenfauna des Dogger, insbesondere des Ober-Bajocium der westlichen Keltiberischen Ketten (Spanien). – Stuttgarter Beiträge zur Naturkunde, Serie B, **14**: 21 pp.

DIETL, G. (1977): The Braunjura (Brown Jurassic) in Southwest Germany. – Stuttgarter Beiträge zur Naturkunde, Serie B, **25**: 41 pp.

DIETL, G. (1982): Das wirkliche Fundniveau von *Ammonites aspidoides* OPPEL (Ammonoidea, Mittl. Jura) am locus typicus. – Stuttgarter Beiträge zur Naturkunde, Serie B, **87**: 21 pp.

DIETL, G. (1986): Erstnachweis von *Oecoptychius subrefractus* (S. BUCKM.) (Ammonoidea) aus dem Unter-Bathonium (Mittl. Jura) von SW-Deutschland. – Stuttgarter Beiträge zur Naturkunde, Serie B, **119**: 13 pp.

DIETL, G., FRANZ, M. & REIS, H. v. (1984): Das Mittel- und Oberbajocium im Gebiet der Wutach unter besonderer Berücksichtigung der *pinguis*-Subzone, basale *humphriesianum*-Zone (Mitteljura, SW-Deutschland). – Jahresberichte und Mitteilungen des oberrheinischen geologischen Vereins, neue Folge, **84**: 307–320.

DIETL, G. & HUGGER, R. (1979): Zur Stratigraphie des Ober-Bajocium (Braunjura δ/ε-Grenzschichten) der Zollernalb (Schwäbische Alb, Baden-Württemberg). – Stuttgarter Beiträge zur Naturkunde, Serie B, **43**: 14 pp.

DIETL, G. & PAVIA, G. (1984): Proposals to the definition of the base of the Upper Bajocian. – In: ZEISS, A. & MICHELSEN, O. (eds.): International Symposium on Jurassic Stratigraphy, Erlangen, September 1st–8th, 1984, Symposium volume, **2**: 328–332; Copenhagen (Geological Survey of Denmark).

DIETL, G. & RIEBER, H. (1980): Der Braune Jura der Westalb zwischen Balingen und Geisingen (Exkursion F1 am 10. April und Exkursion F2 am 11. April 1980). – Jahresberichte und Mitteilungen des Oberrheinischen geologischen Vereins, neue Folge, **62**: 57–69.

DIETZE, V. (2000): Feinstratigraphie und Ammonitenfauna der Acris-Subzone (Parkinsoni-Zone, Ober-Bajocium, Mittlerer Jura) am Ipf (östliche Schwäbische Alb, Süddeutschland). – Stuttgarter Beiträge zur Naturkunde, Serie B, **295**: 43 pp.

DIETZE, V., CALLOMON, J. H., SCHWEIGERT, G. & CHANDLER, R. B. (2005): The ammonite fauna and biostratigraphy of the Lower Bajocian (Ovale and Laeviuscula zones) of E Swabia (S Germany). – Stuttgarter Beiträge zur Naturkunde, Serie B, **353**: 82 pp.

DIETZE, V., CHANDLER, R. B. & CALLOMON, J. H. (2007): The Ovale Zone (Lower Bajocian, Middle Jurassic) at Little Down Wood (Dundry Hill, Somerset, SW England). – Stuttgarter Beiträge zur Naturkunde, Serie B, **368**: 45 pp.

DIETZE, V. & DIETL, G. (2006): Feinstratigraphie und Ammoniten-Faunenhorizonte im Ober-Bajocium und Bathonium des Ipf-Gebietes (Schwäbische Alb, Südwestdeutschland). – Stuttgarter Beiträge zur Naturkunde, Serie B, **360**: 51 pp.

DIETZE, V., ERMER, G., GÖRLICH, M., IVANKIC, Z., KRIEGER, T. & RÖPER, M. (2004): Das Bajocium und Bathonium (Mittel-Jura) bei Greding (Fränkische Alb, Süddeutschland). – Archaeopteryx, **22**: 61–74.

DIETZE, V., SCHWEIGERT, G., CALLOMON, J. H. & GAUTHIER, H. (2002): Garantiana- und frühe Parkinsoni-Zone (Ober-Bajocium, Mittlerer Jura) am Ipf (östliche Schwäbische Alb, SW-Deutschland) mit Bemerkungen zur Phylogenie der Ammonitengattung *Garantiana* MASCKE, 1907. – Stuttgarter Beiträge zur Naturkunde, Serie B, **315**: 89 pp.

DIETZE, V. & STOLMAR, M. (1990): Die Normandie für Fossiliensammler, 2. Teil. – Fossilien, **1990/4**: 163–168.

DI STEFANO, P., GALÁCZ, A., MALLARINO, G., MINDSZENTY, A. & VÖRÖS, A. (2002): Birth and early evolution of a Jurassic escarpment: Monte Kumeta, Western Sicily. – Facies, **46**: 273–298.

DOLLFUSS, S. (1961): Über das Alter des Blegi-Ooliths in der Glärnisch-Gruppe. – Mitteilungen der naturforschenden Gesellschaft des Kantons Glarus, **11**: 91–108.

DONOVAN, D. T., CALLOMON, J. H. & HOWARTH, M. K. (1981): Classification of Jurassic Ammonitina. – In: HOUSE, M. R. & SENIOR, J. R. (eds.): The Ammonoidea. – Systematic Association, special Volume, **18**: 101–155.

DORÉ, F., PAREYN, C., LARSONNEUR, C., RIOULT, M. & JUIGNET, P. (1987): Normandie Maine (deuxième edition). – Guides géologiques régionaux, 216 pp.; Paris (Masson).

DORN, P. (1935): Die Hammatoceraten, Sonninien, Ludwigien, Dorsetensien und Witchellien des süddeutschen, insbesondere fränkischen Doggers. – Palaeontographica, Abteilung A, **82**: 1–124.

DOUVILLÉ, H. (1884): Sur quelques fossiles de la zone à *Amm. Sowerbyi* des environs de Toulon. – Bulletin de la Societé géologique de la France, troisième série, **13**: 12–44.

DOUVILLÉ, H. (1916): Les terrains secondaires dans le Massif du Moghara à l'Est de l'Isthme de Suez, d'après les explorations de M. Couyat-Barthoux. Paléontologie. – Mémoires de l'Academie des Sciences Paris, **2** (**54**): 1–184.

DOUVILLÉ, R. (1906–1910): Palaeontologia Universalis. 200 pp.; Laval (Goupil).

DUGUÉ, O., FILY, G. & RIOULT, M. (1998): Le Jurassique des Côtes du Calvados. Biostratigraphie, sédimentologie, paléoécologie, paléogéographie et stratigraphie séquentielle. – Bulletin trimestriel de la Sociéte géologique de Normandie et des Amis du Muséum du Havre, **85** (2, 2): 1–132.

ELMI, S. (1967): Le Lias supérieur et le Jurassique moyen de l'Ardèche. – Documents du Laboratoire de Géologie du Faculté des Sciences Lyon, **19**: 1–845.

ELMI, S. & RULLEAU, L. (1993): Le Jurassique du Beaujolais méridional, bordure orientale du Massif Central, France. – Géobios, Mémoire spécial, **15**: 139–155.

ENAY, R., GAUTHIER, H., TREVISAN, M., BERTON, J.-B., BRIVET, L., BRODBECK, J.-L., DEMAIZIERES, J.-F., DONIE, P., FOUREL, A. & TREHOUR, M. (2001): Les *Micromphalites* (Ammonitina) du Bathonien inférieur de la Nièvre (France): installation sur la marge européenne de la Téthys de formes sud-téthysiennes d'origine arabique et description d'un néotype de *M. busqueti* (DE GROSS.). – Revue de Paléobiologie, **20**: 503–524.

Enay, R., Mangold, C., du Dresnay, R. & Rakus, M. (1987): Arrivals of Arabian origin among the ammonite faunas of Morocco during the Bajocian-Bathonian. – Palaeogeography, Palaeoclimatology, Palaeoecology, **61**: 107–120.

Engel, T. (1908): Geognostischer Wegweiser durch Württemberg, 3rd edition. XXXI + 645 pp.; Stuttgart (Schweizerbart).

Fallot, P. & Blanchet, F. (1923): Observations sur la faune des terrains Jurassiques de la région de Cardó et de Tortosa (Province de Tarragone). – Treballs Instituto Catalana de Historia naturale, **6**: 73–263.

Fernández López, S. (1977): Nuevos datos estratigráficos sobre el Bajociense inferior en Moscardón (Teruel). – Boletin de la Real Sociedad Española de Historia Natural (Geología), **75**: 45–56.

Fernández López, S. (1982): La Biozona Garantiana (Bajociense, Jurasico Medio) en la region de Tivenys-Sierra de Cardó (Tarragona). – Estudios geologicos, **38**: 75–93.

Fernández López, S. (1985): El Bajociense en la Cordillera Ibérica. 848 + 23 pp.; Madrid (Facultad de Ciencias Géologicas, Departamento de Paleontología, Universidad Complutense).

Fernández López, S. (1988): El Bajociense superior y Bathoniense inferior en Mataporquera (Santander). – Ciencias de la Tierra, Geología, **11**: 73–84.

Fernández López, S. (2000): Lower Bathonian ammonites of Serra de la Creu (Catalanian Basin, Spain). – Revue de Paléobiologie, Volume spéciale, **8**: 45–52.

Fernández López, S. & Aurell, M. (1988): El Bajociense y Bathoniense de Ricla (Zaragoza): Caracteristicas bioestratigráficas y sedimentologicas. – Ciencias de la Tierra, Geología, **11**: 251–264.

Fernández López, S., Aurell, M., García Joral, F., Gómez, J. J., Paiva Henriques, M. H., Martínez, G. & Meléndez, G. (1998a): La Plataforma da Tortosa (Cuenca catalana) durante el Jurásico Medio: unidades litoestratigráficas, paleogeografía y ciclos ambientales. – Cuaderos de Geologia Iberica, **24**: 185–281.

Fernández López, S., Aurell, M., García Joral, F., Gómez, J. J., Paiva Henriques, M. H., Martínez, G., Meléndez, G. & Suárez Vega, L. C. (1997): El Jurásico Medio en la Plataforma de Tortosa (Cuenca Catalana): unidades litoestratigráficas, paleogeografía y ciclos ambientales. – Publicaciones del Seminario de Paleontología de Zaragoza, **3**: 177–213.

Fernández López, S., Chong, G., Quinzio, L. A. & Wilke, H.-G. (1994): The Upper Bajocian and Bathonian in the Cordillera de Domeyko, North-Chilean Precordillera: Sedimentological and biostratigraphical results. – Géobios, Mémoires spéciales, **17**: 187–201.

Fernández López, S., García Joral, F., Gómez, J. J., Henriques, M. H. P. & Martínez, G. (1998b): La diferenciación paleogeográfica de la Cuenca Catalana al principio del Jurásico Medio. – Revista de la Sociedad Geológica de España, **11**: 3–22.

Fernández López, S. & Gómez, J. J. (1990): Evolution tectono-sedimentaire et genese des associations d'ammonites dans le secteur central du Bassin Iberique (Espangne) pendant l'Aalenien. – Cahiers de l'Université Catholique de Lyon, **4**: 39–52.

Fernández López, S., Gómez, J. J. & Ureta, M. S. (1988a): Caracteristicas de la plataforma carbonadata del Dogger en el sector meridional de la Sierra de la Demanda (Soria). – Ciencias de la Tierra, Geología, **11**: 167–195.

Fernández López, S., Goy, A. & Ureta, M. S. (1988b): El Toarciense superior, Aaleniense y Bajociense en Camino (Santander). Precisiones bioestratigráficos. – Ciencias de la Tierra, Geología, **11**: 47–62.

Fernández López, S., Henriques, M. H., Mouterde, R., Rocha, R. & Sadki, D. (1988c): Le Bajocien inferieur du Cap Mondego (Portugal) – essai de Biozonation. – In: Rocha, R. B. & Soares, A. F. (eds.): 2nd International Symposium on Jurassic Stratigraphy, **1**: 301–313; Lisboa.

Fernández López, S. & Mouterde, R. (1994a): L'Horizon à *Gervillii* (Bajocien inférieur) de Tendron (Cher, France). Taphonomie et populations d'Ammonites. – Miscellanea del Servizio Geologico Nazionale, **5**: 117–159.

Fernández López, S. & Mouterde, R. (1994b): Observations taphonomiques et paléontologiques sur l'association d'ammonites de l'Horizon à Gervillii (Bajocien Inférieur) de Tendron (Cher, France). – Cahiers de l'Université Catholique de Lyon, **10**: 147–157.

Fernández López, S. & Suárez-Vega, L. C. (1979): Estudio bioestratigráfico (Ammonoidea) del Aaleniense y Bajociense en Asturias. – Cuadernos Geologicos, **10**: 1–12.

Fischer, J.-C. (1994): Révision critique de la Paléontologie française d'Alcide d'Orbigny. **1**. Céphalopodes jurassiques. XII+340 pp.; Paris, Milan & Barcelona (Masson).

Flamand, G. B. M. (1911): Recherches géologiques et géographiques sur "Le Haut-Pays de l'Oranie" et sur le Sahara (Algérie et territoires du Sud). – Thèses du Faculté des Sciences de l'Université de Lyon, **47**: 1001 pp.; Paris (Monrocq).

Galácz, A. (1970): Biostratigraphic investigation of the Middle Jurassic of Gyenespuszta, northern Bakony, Transdanubian Central Mountains, Hungary. – Annales Universitatis Scientiarium Budapestiniensis de Rolando Eötvös nominatae, sectio Geologica, **13**: 109–128.

Galácz, A. (1976): Bajocian (Middle Jurassic) sections from the Northern Bakony (Hungary). – Annales Universitatis Scientiarium Budapestiniensis de Rolando Eötvös nominatae, sectio Geologica, **18**: 177–191.

Galácz, A. (1980): Bajocian and Bathonian ammonites of Gyenespuszta, Bakony Mts., Hungary. – Geologica Hungarica, series Palaeontologica, **39**: 1–151.

Galácz, A. (1988): The boundaries and a proposed subdivision of the Bajocian *Otoites sauzei* zone. – In: Rocha, R. B. & Soares, R. F. (eds.): 2nd International Symposium on Jurassic Stratigraphy, Lisboa, **1**: 215–231; Lisboa.

Galácz, A. (1991): Lower Bajocian sonninid ammonites from the Gerecse Mountains, Hungary. – In: Morton, N. (ed.): Proceedings of the conference on Aalenian and Bajocian stratigraphy, Isle of Skye, Scotland: 109–111; London (Birkbeck College).

Galácz, A. (1999): A Lower Bathonian ammonite fauna from Erice (Western Sicily). – Annales Universitatis Scientiarium Budapestiniensis de Rolando Eötvös nominatae, sectio Geologica, **32**: 149–168.

Gassmann, G. & Ohmert, W. (1990): Der Humphriesi-Oolith von Egerten im Wollbachtal (Oberrheingebiet). – Jahreshefte des Geologischen Landesamts Baden-Württemberg, **32**: 159–170.

Gauthier, H., Branger, P., Boursicot, P.-Y., Trévisan, M. & Marchand, D. (2002): La faune d'*Orthogarantiana* Bentz (Garantianinae, Stephanoceratidae) de la sous-zone à Polygyralis (z. à Niortense, Bajocien sup.) nouvellement découverte au nord de Niort (Deux-Sèvres, France). Une preuve du dimorphisme *Orthogarantiana/Strenoceras*. – Géologie de la France, **2002**: 81–86.

Gauthier, H., Rioult, M. & Trévisan, M. (1995): Enregistrement biostratigraphique exceptionnel dans l'"Oolithe ferrugineuse de Bayeux" au Sud de Caen (Normandie, France): complément au stratotype du Bajocien. – Comptes Rendues de l'Académie de Science, Paris, série 2a, **321**: 317–323.

Gauthier, H., Rioult, M. & Trévisan, M. (1996): Répartition biostratigraphique des ammonites dans l'Oolithe ferrugineuse de Bayeux (Bajocien) à Feuguerolles-sur-Orne (Calvados). Eléments nouveaux pour une révision des Garantianinae. – Géologie de la France, **1996** (2): 27–67.

Géczy, B. (1967): Ammonoides jurassiques de Csernye, Montagne Bakony, Hongrie, Part II (excl. Hammatoceratidae). – Geologica Hungarica, series Palaeontologica, **35**: 1–413.

Géczy, B. (1971): Biozones et chronozones dans le Jurassique de Csernye. – Mémoires du Bureau de recherches géologiques et minières, **75**: 411–422.

Gómez-Alba, J. A. S. (1988): Guía de Campo de los fósiles de España y de Europa. XLIV + 925 pp.; Barcelona (Omega).

Greppin, E. & Tobler, A. (1929): Zur Geologie und Paläontologie des Flexurgebiets von Stetten-Lörrach. – Verhandlungen der naturforschenden Gesellschaft Basel, **40** (2): 536–587.

Hall, R. L. & Westermann, G. E. G. (1980): Lower Bajocian (Jurassic) cephalopod faunas from western Canada and proposed assemblage zones for the Lower Bajocian of North America. – Palaeontographica Americana, **9** (52): 1–93.

Haug, E. (1891): Les Chaînes Subalpines entre Gap et Digne. – Bulletin de la Service du Carte géologique de France, **3** (21): 192 pp.

Hegele, A. (1990): Der Albaufstieg am Aichelberg. – Der Aufschluss, **41**: 313–320.

Hegele, A. (1995): Überraschungen an der Autobahn. – Fossilien, **12**: 216–228.

Hillebrandt, A. v., Westermann, G. E. G., Callomon, J. H. & Detterman, R. L. (1997):

Ammonites of the circum-Pacific region. – In: WESTERMANN, G. E. G. (ed.): Jurassic of the Circum-Pacific: 342–359; New York (Cambridge University Press).

HINKELBEIN, K. (1975): Beiträge zur Stratigraphie und Paläontologie des Jura von Ostspanien. VIII. Stratigraphie und Fazies im Mitteljura der zentralen Iberischen Ketten. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **148**: 139–184.

HÖLDER, H. (1964): Jura. – Handbuch der stratigraphischen Geologie, **4**: XV + 603 pp.; Stuttgart (Enke).

HUF, W. (1968): Über Sonninien und Dorsetensien aus dem Bajocium von Nordwestdeutschland. – Beihefte zum Geologischen Jahrbuch, **64**: 1–168.

HUXTABLE, J. G. (1991): A further examination of the Subfurcatum Zone (Middle Jurassic; Upper Bajocian) of North Dorset. – Proceedings of the Dorset natural History and archaeological Society, **113**: 196–198.

HUXTABLE, J. G. (2000): A review of the stratigraphy of the Inferior Oolite (Bajocian Stage, Middle Jurassic) near Clatcombe, Sherborne, with a description of temporary sections. – Proceedings of the Dorset natural History and archaeological Society, **121**: 101–106.

HUXTABLE, J. G. (2006): A description of a permanent new section and of nearby temporary sections in the Inferior Oolite (Bajocian Stage, Middle Jurassic) of Milborne Wick, Somerset. – Proceedings of the Dorset natural History and archaeological Society, **127**: 77–85.

IMLAY, R. W. (1961): New genera and subgenera of Jurassic (Bajocian) ammonites from Alaska. – Journal of Paleontology, **35**: 467–474.

IMLAY, R. W. (1964): Middle Bajocian ammonites from the Cook Inlet region, Alaska. – United States Geological Survey, professional paper, B, **418**: 1–61.

IMLAY, R. W. (1973): Middle Jurassic (Bajocian) ammonites from Eastern Oregon. – United States Geological Survey, professional paper, **756**: 1–100.

IMLAY, R. W. (1980): Middle Jurassic (Bathonian) ammonites from southern Alaska. – United States Geological Survey, professional paper, **1091**: 1–42.

International Commission on Zoological Nomenclature (2005): Opinion 2123 (case 999). – Bulletin of Zoological Nomenclature, **62**: 158–163.

JAWORSKI, E. (1926): La fauna del Lias y Dogger de la Cordillera Argentina en la parte meridional de la Provincia de Mendoza. – Actas de la Academia Nacional de Ciencias en Córdoba, **9**: 139–317.

KOKEN, E. (1896): Die Leitfossilien. 847 pp.; Leipzig (Tauchnitz).

KROBICKI, M. & WIERZBOWSKI, A. (2004): Pozycja stratygraficzna i paleogeograficzne znaczenie bajoskich wapieni krynoidowych w ewolucji pienińskiego basenu skałkowego. – Volumina Jurassica, **2**: 69–82.

KRYMHOLTZ, H. I. & STANKEWITCH, E. S. (1963): Some Bathonian ammonites from Daghestan. – USSR Academy of Sciences, Karpinski Geological Museum, **14**: 107–114. – [In Russian]

KRYSTYN, L. (1971): Stratigraphie, Fauna und Fazies der Klaus-Schichten (Aalenium-Oxford) in den Östlichen Nordalpen. – Verhandlungen der Geologischen Bundes-Anstalt, **1971**: 486–509.

KRYSTYN, L. (1972): Die Ober-Bajocium und Bathonium-Ammoniten der Klaus-Schichten des Steinbruches Neumühle bei Wien (Österreich). – Annalen des Naturhistorischen Museums Wien, **76**: 195–310.

KUHN, O. (1933): Zur Kenntnis der Cephalopodengattung *Cymaceras* HYATT. – Paläontologische Zeitschrift, **15**: 318–321.

KUMM, A. (1952): Das Mesozoikum in Niedersachsen: Der Dogger. – Geologie und Lagerstätten Niedersachsens, **2**: 329–509; Bremen (Dorn).

LANQUINE, A. (1929): Le Lias et le Jurassique des chaînes provençales. – Bulletin des Services de la Carte Géologique de la France et des Topographies Souterraines, **32** (173): 385 pp.

LINARES, A. & SANDOVAL, J. (1979): Contributión al estudio del Bajocense de la Sierra de Ricote (Murcia). – Cuadernos Geología, **8**: 275–308.

LINARES, A. & SANDOVAL, J. (1990): The lower boundary of the Bajocian in the "Barranco de Agua Larga" section (Subbetic Domain, Southern Spain). – Memorie descrittive della Carta geologica d'Italia, **40**: 13–22.

LINARES, A. & SANDOVAL, J. (1993): El Aaleniense de la Cordillera Bética (Sur de España): análisis bioestratigrafico y caracterizacion paleogeografica. – Revista de la Sociedad geológica de España, **6**: 177–206.

LISSAJOUS, M. (1906): Bajocien et Bathonien des environs de Mâcon. – Bulletin de la Societé géologique de France, **44**: 689–698.

LISSAJOUS, M. (1907–1912): Jurassique Mâconnais: Descriptions des fossiles caractéristiques et des espèces le plus communes. – Bulletin de la Societé d'histoire naturelle de Mâcon, **3**: 208 pp.

LÓCZY, L. (1915): Monographie der Villányer Callovien-Ammoniten. – Geologica Hungarica, **1** (3–4): 255–502.

LUPHER, R. L. (1941): Jurassic stratigraphy of central Oregon. – Bulletins of the Geological Society of America, **52**: 219–269.

MAKOWSKI, H. (1963): Problem of sexual dimorphism in ammonites. – Palaeontologica Polonica, **12**: 1–92.

MATYJA, B. A. & WIERZBOWSKI, A. (2000): Ammonites and stratigraphy of the uppermost Bajocian and Lower Bathonian between Częstochowa and Wieluń, Central Poland. – Acta Geologica Polonica, **50**: 191–209.

MAUBEUGE, P. L. (1951): Les ammonites du Bajocien de la région frontière Franco-Belge (bord septentrional du Bassin de Paris). – Mémoires de l'Institute Royale de Sciences naturelles Belgique, série 2, **42**: 1–104.

MAUBEUGE, P. L. (1955): Les ammonites Aaléniennes, Bajociennes et Bathoniennes du Jura Suisse septentrional. – Schweizerische Paläontologische Mitteilungen, **71**: 1–48.

MAUBEUGE, P. L. (1967): Catalogue des Ammonites du Jurassique inférieur et moyen (Hettangien à Bathonien) du Musée cantonal de Bâle-Campagne. Deuxième partie. – Tätigkeitsberichte der naturforschenden Gesellschaft Baselland, **25**: 43–130.

MENCHIKOFF, N. (1936): Études géologiques sur les confers Algéro-Marocain du Sud. – Bulletin de la Societé géologique de France, cinquième série, **6**: 131–148.

MENSINK, H. (1965): Stratigraphie und Paläogeographie des marinen Jura in den nordwestlichen Iberischen Ketten (Spanien). – Beihefte zum geologischen Jahrbuch, **44**: 55–102.

MIHAJLOVIC, M. (1969): Klauska ammonitska fauna dogera okoline Donjeg Milanovca (Ist. Srbija). – Bulletin du muséum d'histoire naturelle Belgrade, série A, **24**: 45–125.

MITTA, V. V. (2004): *Sokurella galaczi* gen. et sp. nov. and other Middle Jurassic Parkinsoniidae (Ammonoidea) from the lower banks of the Volga River. – Paleontological Journal, **38**: 257–264.

MORTON, N. (1975): Bajocian Sonniniidae and other ammonites from western Scotland. – Palaeontology, **18**: 41–91.

MORTON, N. (1976): Bajocian (Jurassic) stratigraphy in Skye, Western Scotland. – Scottish Journal of Geology, **12**: 23–33.

MOUTERDE, R. (1953): Études sur le Lias et le Bajocien des bordures Nord et Nord-Est du Massif Central français. – Bulletin du Service de la Carte géologique de la France, tome 50, **236**: 457 pp.

MOUTERDE, R. (1991): Données paléontologiques sur les ammonites de la limite Aalénien-Bajocien présentées à Piobicco (1988). – In: MORTON, N. (ed.): Conference on Aalenian and Bajocian stratigraphy, Isle of Skye: 125–129; London (Birkbeck College).

MOYNE, S. & NEIGE, P. (2004): Cladistic analysis of the Middle Jurassic ammonite radiation. – Geological Magazine, **141**: 115–123.

MOYNE, S., NEIGE, P., MARCHAND, D. & THIERRY, J. (2004): Répartition mondiale d'ammonites au Jurassique moyen (Aalénien supérieur à Bathonien moyen): relations entre biodiversité et paléogéographie. – Bulletin de la Societé géologique de France, **175**: 513–523.

MUNIER-CHALMAS, E. C. P. A. (1892): Sur la possibilité d'attmettre un dimorphisme sexuel chez les Ammonitides. – Comptes rendues de la Societé géologique de France, troisième série, **20**: 170–174.

NEUMAYR, M. (1878): Über unvermittelt auftretende Cephalopoden-Typen im Jura Mittel-Europas.– Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt, **28**: 37–80.

OHMERT, W. (1988): Das Unter-Bajocium von Badenweiler (Oberrhein), verglichen mit Nachbargebieten. – Jahreshefte des Geologischen Landesamts Baden-Württemberg, **30**: 315–347.

OHMERT, W. (1990): The *Humphriesianum* Zone in the type area. – Memorie descrittive della Carta geologica d'Italia, **40**: 117–140.

OHMERT, W., GASSMANN, G., SCHATZ, R. H. & STETTER, I. (1995): Das höhere Unter-Bajocium von Lörrach. II. Die *humphriesianum*-Zone. – Jahreshefte des Geologischen Landesamts Baden-Württemberg, **35**: 25–264.

Ooster, W. A. (1860): Catalogue des céphalopodes fossiles des Alpes Suisses avec la description et les figures des espèces remarquables, 4ème partie, Céphalopodes tentaculifères, Ammonitides, G. *Ammonites*. – Denkschriften der Schweizerischen naturforschenden Gesellschaft, **18**: 1–160.

Oppel, A. (1856): Die Juraformation Englands, Frankreichs und des südwestlichen Deutschlands. – Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, **12**: 121–556.

Orbigny, A. de (1842–1851): Paléontologie Française. Description zoologique et géologique de tous les animaux mollusques et rayonnés fossiles de France, comprenant leur application à la reconnaissance des couches. Terrains oolithiques ou jurassiques, 1, Céphalopodes. 624 pp.; Paris (Masson).

Parona, C. F. (1896): Nuove osservazioni sopra la faune e l'età degli strati con *Posidonomya alpina* nei Sette Comuni. – Palaeontographia Italica, **1**: 1–42.

Parsons, C. F. (1974): The *sauzei* and "so called" *sowerbyi* zones of the Lower Bajocian. – Newsletters in Stratigraphy, **3**: 153–180.

Parsons, C. F. (1975): The stratigraphy of the Stony Head Cutting. – Proceedings of the Dorset natural History and archaeological Society, **96**: 8–13.

Parsons, C. F. (1976): A stratigraphic revision of the humphriesianum/subfurcatum Zone rocks (Bajocian Stage, Middle Jurassic) of Southern England. – Newsletters in Stratigraphy, **5**: 114–142.

Parsons, C. F. (1977): Two new Bajocian microconch otoitid ammonites and their significance. – Palaeontology, **20**: 101–118.

Parsons, C. F. (1979): A stratigraphic revision of the Inferior Oolite at Dundry Hill, Bristol. – Proceedings of the Geologists' Association, **90**: 133–151.

Pavia, G. (1969): Nouvelles données sur le Bajocien de Digne (Basses-Alpes). – Bollettino della Società geologica Italiana, **88**: 445–451.

Pavia, G. (1973): Ammoniti del Baiociano superiore di Digne (Francia SE, dip. Basses-Alpes). – Bollettino della Società paleontologica Italiana, **10**: 75–142.

Pavia, G. (1983): Ammoniti e biostratigrafia del Baiociano inferiore di Digne. – Monografia di Museo regionale et Scienze naturale di Torino. 257 pp.

Pavia, G. (2006): Nomenclatural suitability in ammonoid classification: generic *versus* subgeneric status of dimorphic pairs. – Volumina Jurassica, **4**: 241–242.

Pavia, G. & Cresta, S. (2002): Revision of Jurassic ammonites of the Gemmellaro collections. – Quaderno Museo Geologico "G. G. Gemmellaro", **6**: 406 pp.

Pavia, G. & Martire, L. (1998): The importance of taphonomic studies on biochronology: Examples from the European Middle Jurassic. – Cuadernos de Geología Ibérica, **23**: 153–181.

Pavia, G. & Sturani, C. (1968): Étude biostratigraphique du Bajocien des Chaînes Subalpines aux environs de Digne (Basses-Alpes). – Bollettino della Società geologica Italiana, **87**: 305–316.

Poulton, T. P., Detterman, R. L., Hall, R. L., Jones, D. L., Peterson, J. A., Smith, P., Taylor, D. G., Tipper, H. W. & Westermann, G. E. G. (1992): Western Canada and United States. – In: Westermann, G. E. G. (ed.): Jurassic of the Circum-Pacific: 29–92; New York (Cambridge University Press).

Prinz, G. (1904): Die Fauna der älteren Jurabildungen im nordöstlichen Bakony. – Mitteilungen aus dem Jahrbuche der königlich Ungarischen geologischen Anstalt, **25** (1): 1–142.

Quenstedt, F. A. (1856–1858): Der Jura. 842 pp.; Tübingen (Laupp).

Quenstedt, F. A. (1886–1887): Die Ammoniten des Schwäbischen Jura. **2**. Der Braune Jura: 441–815; Stuttgart (Schweizerbart).

Richter, A. E. (1982): Ammoniten. 139 pp.; Stuttgart (Kosmos).

Richter, A. E. (2003): Strigoceras aus dem Calvados. – Fossilien, **20**: 331.

Rioult, M. (1964): Le stratotype du Bajocien. – In: Colloque Jurassique Luxembourg, 1962. – Publications de l'Institute Grand-Duchesse de Luxembourg, Section Sciences naturelles, Physique, Mathématique, pp. 239–258.

Rioult, M. (1971): Observations sur le stratotype du Bajocien et sur l'etage Bajocien de A. d'Orbigny. – Mémoires du Bureau de recherches géologiques et minières, **75**: 375–383.

RIOULT, M., CONTINI, D., ELMI, S. & GABILLY, J. (1997): Bajocien. – In: CARIOU, É. & HANTZPERGUE, P. (eds.): Biostratigraphie du Jurassique ouest-européen et méditerranéen. – Bulletin du Centre de Recherche Elf Exploration et Production, Mémoires, **17**: 41–54.

ROCHA, R. B., HENRIQUES, M. H., SOARES, A. F., MOUTERDE, R., CALOO, B., RUGET, C. & FERNÁNDEZ LÓPEZ, S. (1990): The Cabo Mondego Section as a possible Bajocian boundary stratotype. – Memorie descrittive della Carta geologica d'Italia, **40**: 49–69.

ROCHÉ, P. (1939): Aalénien et Bajocien du Maconnais et de quelques régions voisines. – Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon, **35**/29: 1–255.

ROMAN, F. (1938): Les ammonites jurassiques et crétacées. Essai de génera. 554 pp.; Paris (Masson).

ROMAN, F. & GENNEVAUX, M. (1912): Études sur les terrains jurassiques de la région du Pic-Loup. Fasc. 1. Jurassique inferieur et moyen (Lias, Aalénien, Bajocien, Bathonien). 101 pp.; Montpellier (Valat).

ROMAN, F. & PÉTOURAUD, C. (1927): Étude sur la faune du Bajocien superieur du Mont d'Or Lyonnais (Ciret) – I. Cephalopodes. – Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon, 11/9: 5–55.

ROSTOVTSEV, K. O. (1985): Ammonoidea. – In: ROSTOVTSEV, K. O., PROSOROVSKAJA, E. L., VUKS, W. & BELENKOVA, W. S. (eds.): The Jurassic deposits of the south part of the Transcaucasus: 117–168; Leningrad (NAUKA). – [In Russian]

ROSTOVTSEV, K. O. (1992): Jurassic of Caucasus. – Russian Academy of Sciences, Committee on Geology and Exploitation of National resources, Interdepartmental Stratigraphic Committee, Transactions, **22**: 1–184. – [In Russian]

RULLEAU, L. (1997): Les Fossiles du Bajocien de la région Lyonnaise. 13 pp.; Lozanne (Comité d'Entreprise des Ciments Lafarge édition).

RULLEAU, L. (2006): Biostratigraphie et paléontologie du Lias supérieur et du Dogger de la région lyonnaise. 382 pp.; Lozanne (Comité d'Entreprise des Ciments Lafarge édition).

SADKI, D. (1994a): L'Aalenian supérieur et le Bajocien inférieur du Haut-Atlas marocain: révision biostratigraphique et corrélations. – Miscellanea del Servizio Geologico Nazionale, **5**: 177–190.

SADKI, D. (1994b): La région de Rich (Haut-Atlas central marocain), une des localités types pour le choix de la limite Aalenien – Bajocien. – Miscellanea del Servizio Geologico Nazionale, **5**: 313–321.

SADKI, D. (1996): Le Haut-Atlas Central (Maroc). Stratigraphie et paléontologie du Lias supérieur et du Dogger inférieur. Dynamique du bassin et des peuplements. – Documents des Laboratoires de Géologie Lyon, **142**: 1–225.

SADKI, D., IBNOUSSINA, M. & MOUTERDE, R. (1986): Biostratigraphie des ammonites du sommet de l'Aalenien et du Bajocien inférieur dans le Haut-Atlas Central, Maroc. – Revue de la Faculté des Sciences de Marrakech, numéro spéciale, **2**: 443–462.

SALVADOR, A., WESTERMANN, G. E. G., OLÓRIZ, F., GORDON, M. B. & GURSKY, H.-J. (1992): Meso-America. – In: WESTERMANN, G. E. G. (ed.): The Jurassic of the Circum-Pacific: 93–121; New York (Cambridge University Press).

SANDOVAL, J. (1979): El Bajocense en la Zona Subbetica. – II Coll. Estratigrafía y Paleogeografía del Jurassico del España, 1979. – Quadernos geologicos de l'Universidad de Granada, **10**: 425–462.

SANDOVAL, J. (1983): Bioestratigrafía y Paleontología (Stephanocerataceae y Perisphinctaceae) del Bajocense y Bathonense en las Cordilleras Béticas. –Tesis Doctoral Universidad de Granada. 613 pp.; Granada. – [Unpubl.]

SANDOVAL, J. (1985): Los Strigoceratidae (Ammonitina) del Bajocense de la Zona Subbétcia (Sur de Espana). – Mediterránea, serie de estudios geologicos, **4**: 85–112.

SANDOVAL, J. (1986): Middle Jurassic Haploceratidae (Ammonitina) from the Subbetic Zone (South Spain). – Géobios, **19**: 435–463.

SANDOVAL, J. (1990): A revision of the Bajocian divisions in the Subbetic Domain (southern Spain). – Memorie descrittive della Carta geologica d'Italia, **40**: 141–162.

SANDOVAL, J. (1994): The Bajocian stage in the Island of Majorca: biostratigraphy and ammonite assemblages. – Miscellanea del Servizio Geologico Nazionale, **5**: 203–215.

SANDOVAL, J. & WESTERMANN, G. E. G. (1986): The Bajocian (Jurassic) ammonite fauna of Oaxaca, Mexico. – Journal of Paleontology, **60**: 1220–1271.

Santantonio, M. (2002): General Field Trip Guidebook. VI International Symposium on the Jurassic System, 12–22 September 2002. 320 pp.; Palermo.

Sato, T. (1962): Études biostratigraphiques des Ammonites du Jurassique du Japon. – Mémoires de la Societé géologique de France, nouvelle série, **41**: 1–122.

Sato, T. (1972): Some Bajocian ammonites from Kitakami, northeast Japan. – Transactions and proceedings of the Palaeontological Society of Japan, new series, **85**: 280–292.

Sato, T. & Westermann, G. E. G. (1991): Japan and South-East Asia. – In: Westermann, G. E. G. & Riccardi, A. C. (eds.): Jurassic taxa ranges and correlation charts for the Circum Pacific. – Newsletters in Stratigraphy, **24**: 81–108.

Schairer, G. & Schlampp, V. (1991): *Cymaceras* (Ochetoceratinae) von Esselberg. – Münchner geowissenschaftliche Abhandlungen, Reihe A, **19**: 101–128.

Schatz, R. H. (1985): Ammonitenfunde aus dem tiefen Dogger in Lörrach. – Der Aufschluss, **36**: 283–287.

Scheurlen, H. (1928): *Strigoceras* und *Phlycticeras*. – Palaeontographica, **70**: 1–40.

Schick, H. W. (2004): The stratigraphical significance of *Cymaceras guembeli* for the boundary between the Platynota Zone and Hypselocyclum Zone, and the correlation between Swabian and Franconian Alb. – Zitteliana, A, **44**: 51–59.

Schindewolf, O. H. (1964): Studien zur Stammesgeschichte der Ammoniten. – Abhandlungen der Akademie der Wissenschaften und der Literatur Mainz, mathematisch-naturwissenschaftliche Klasse, **3**: 263–432.

Schlampp, V. (1997): Es muß nicht immer *Parkinsonia* sein. – Fossilien, **14**: 194.

Schlegelmilch, R. (1985): Die Ammoniten des süddeutschen Doggers. 284 pp.; Stuttgart & New York (Fischer).

Schlögl, J. (2002): Sedimentology and biostratigraphy of the "ammonitico rosso" deposits in the Czorsztyn Formation of the Czorsztyn Unit, Pieniny Klippen Belt (Western Carpathians, Slovakia). – PhD Thesis, Faculty of Sciences, University of Bratislava, 196 pp. – [In Slovakian, unpublished]

Schlögl, J. & Rakús, M. (2004): Ammonites of Arabian origin from the Early Bathonian of the Czorsztyn Unit, Pieniny Klippen Belt (Western Carpathians, Slovakia). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **2004**: 449–460.

Schlögl, J., Rakús, M., Mangold, C. & Elmi, S. (2005): Bajocian – Bathonian ammonite fauna of the Czorsztyn Unit, Pieniny Klippen Belt (Western Carpathians, Slovakia); its biostratigraphical and palaeobiogeographical significance. – Acta Geologica Polonica, **55**: 339–359.

Schloenbach, U. (1865): Beiträge zur Paläontologie der Jura- und Kreide-Formation im nordwestlichen Deutschland. I. Ueber neue und weniger bekannte jurassische Ammoniten. – Palaeontographica, **13**: 147–192.

Schweigert, G. (1998): Die Ammonitenfauna des Nusplinger Plattenkalks (Ober-Kimmeridgium, Beckeri-Zone, Ulmense-Subzone, Schwäbische Alb). – Stuttgarter Beiträge zur Naturkunde, Serie B, **267**: 61 pp.

Schweigert, G., Atrops, F., Benetti, A. & Zeiss, A. (1999): The ammonite genera *Oxydiscites* Dacqué, 1934 and *Sphaerodomites* Rollier, 1909 (Ammonitina, Strigoceratidae, Middle – Late Jurassic). – Profil, **16**: 57–71.

Schweigert, G. & Dietze, V. (1998): Revision der dimorphen Ammonitengattungen *Phlycticeras* Hyatt – *Oecoptychius* Neumayr (Strigoceratidae, Mitteljura). – Stuttgarter Beiträge zur Naturkunde, Serie B, **269**: 59 pp.

Schweigert, G. & Dietze, V. (1999): *Oecoptychius* – des Rätsels Lösung. – Fossilien, **16**: 51–58.

Schweigert, G. & Dietze, V. (2004): Die Spiralgestreiften: *Strigoceras* oder *Phlycticeras*? – Fossilien, **21**: 74–75.

Schweigert, G., Dietze, V. & Balle, T. (2000): Dimorphismus und Phylogenie der Ammonitengattung *Csernyeiceras* Géczy (Früher Mitteljura, Phlycticeratinae). – Stuttgarter Beiträge zur Naturkunde, Serie B, **294**: 13 pp.

Schweigert, G., Dietze, V. & Dietl, G. (2002): Erstnachweis der Ammoniten-Gattung *Parkinsonia* Bayle, 1878 in der Garantiana-Zone (Tetragona-Subzone). – Stuttgarter Beiträge zur Naturkunde, Serie B, **320**: 15 pp.

Schweigert, G., Dietze, V. & Dietl, G. (2003): Neue Nachweise von *Phlycticeras* und *Oecoptychius* (Ammonitina: Strigoceratidae: Phlycticeratinae). – Stuttgarter Beiträge zur Naturkunde, Serie B, **335**: 21 pp.

Senior, J. H., Parsons, C. F. & Torrens, H. S. (1970): New sections in the Inferior Oolite of South Dorset. – Proceedings of the Dorset natural History and archaeological Society, **91**: 114–119.

Sequeiros, L., Cólera, I., Valenzuela, R. & Sánchez, I. (1978): Bioestratigrafía del Jurásico (Lias y Dogger) en el sector Belchite – Almonacid de la Cuba (Provincia de Zaragoza, Cordillera Ibérica). – Estudios geologicos, **34**: 293–298.

Seyed-Emami, K. (1988): Eine Ammoniten-Fauna aus der Badamu-Formation (Unterbajocium, *sauzei*-Zone) westlich von Kerman (Zentraliran). – Paläontologische Zeitschrift, **62**: 71–86.

Seyed-Emami, K. & Alavi-Naini, M. (1990): Bajocian stage in Iran. – Memorie descrittive della Carta geologica d'Italia, **40**: 215–222.

Seyed-Emami, K., Schairer, G. & Mohammadi-Monared, M. (1998): Ammoniten aus dem Oberen Jura des Nordiran. – Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie, **38**: 97–110.

Sturani, C. (1964a): Ammoniti mediogiurassiche del Veneto. Faune del Baiociano terminale (zone a *garantiana* e a *parkinsoni*). – Memorie degli Istituti di Geologia e Mineralogia dell'Università di Padova, **24**: 43 pp.

Sturani, C. (1964b): La succesione delle faune ad ammoniti nelle formazioni mediogiurassiche delle Prealpi Venete occidentali. – Memorie degli Istituti di Geologia e Mineralogia dell'Università di Padova, **24**: 78 pp.

Sturani, C. (1971): Ammonites and stratigraphy of the "*Posidonia alpina*" beds of the Venetian Alps. – Memorie degli Istituti di Geologia e Mineralogia dell'Università di Padova, **28**: 1–190.

Taylor, D. C. (1988): Middle Jurassic (late Aalenian and early Bajocian) ammonite biochronology of the Snowshoe Formation, Oregon. – Oregon Geology, **50**: 123–138.

Taylor, D. C. & Smith, P. (1991): Eastern Oregon and adjacent areas. – In: Westermann, G. E. G. (ed.): The Jurassic of the Circum-Pacific: 67–72; New York (Cambridge University Press).

Thierry, J., Cariou, E., Elmi, S., Mangold, C., Marchand, D. & Rioult, M. (1997): Callovien. – In: Cariou, E. & Hantzpergue, P. (eds.): Biostratigraphie du Jurassique ouest-européen et méditerranéen. – Bulletin du Centre de Recherche Elf Exploration et Production, Mémoires, **17**: 63–78.

Torrens, H. S. (1969): Field Meeting in the Sherborne – Yeovil District. – Proceedings of the Geologists' Association, **80**: 301–330.

Trauth, F. (1923a): Über eine Doggerfauna aus dem Lainzer Tiergarten bei Wien. – Annalen des naturhistorischen Museums, **36**: 167–250.

Trauth, F. (1923b): Über die Stellung der "pieninischen Klippenzone" und die Entwicklung des Jura in den niederösterreichischen Voralpen. – Mitteilungen der geologischen Gesellschaft Wien, **14**: 105–265.

Trauth, F. (1928): Geologie der Klippenregion von Ober-St. Veit und des Lainzer Tiergartens. – Mitteilungen der geologischen Gesellschaft Wien, **21**: 35–132.

Verlet, C. & Roch, É. (1940): Compléments à la géologie du Nord de Figuig (Maroc SE). – Bulletin de la Societé géologique de France, cinquième série, **10**: 65–86.

Waagen, W. (1867): Über die Zone des *Ammonites Sowerbyi*. – Geognostisch-paläontologische Beiträge, **1/3** (2): 509–713.

Wendt, J. (1963): Stratigraphisch-paläontologische Untersuchungen im Dogger Westsiziliens. – Bollettino della Società paleontologica Italiana, **2**: 57–145.

Wendt, J. (1971): Genese und Fauna submariner sedimentärer Spaltenfüllungen im mediterranen Jura. – Palaeontographica, Abteilung A, **136**: 122–192.

Westermann, G. E. G. (1954): Monographie der Otoitidae (Ammonoidea): *Otoites*, *Trilobiticeras*, *Itinsaites*, *Epalxites*, *Germanites*, *Masckeites* (*Pseudotoites*, *Polyplectites*), *Normannites*. – Beihefte zum geologischen Jahrbuch, **15**: 1–364.

Westermann, G. E. G. (1955): Biostratigraphische Untersuchungen im Jura südlich der Sierra de la Demanda (Nord-Spanien). – Geologisches Jahrbuch, **70**: 515–534.

Westermann, G. E. G. (1958): Ammoniten-Fauna und Stratigraphie des Bathonien NW-Deutschlands. – Beihefte zum geologischen Jahrbuch, **32**: 1–103.

Westermann, G. E. G. (1992): The Jurassic of the Circum-Pacific. X + 676 pp.; New York (Cambridge University Press).

WETZEL, W. (1924): Beiträge zur Stratigraphie und Ammonitenfauna des mittleren Doggers von Nordwesteuropa. – Palaeontographica, **65**: 155–247.

WHICHER, J. (1969): New sections in the Inferior Oolite near Halfway House, Sherborne, Dorset. – In: TORRENS, H. S. (ed.): Field meeting in N Dorset and S Somerset. – Proceedings of the Geologists' Association, **80**: 324–330.

WHICHER, J. & PALMER, C. P. (1971): Preliminary description of a temporary exposure in the Middle Inferior Oolite, near Sherborne, Dorset. – Proceedings of the Dorset natural History and archaeological Society, **92**: 110–119.

WILSON, V., WELCH, F. B. A., ROBBIE, J. A. & GREEN, G. W. (1958): Geology of the Country around Bridport and Yeovil (Explanation of Sheets 327 and 312). – Memoirs of the Geological Survey of Great Britain. 239 pp.; London (Her Majesty's Stationery Office).

WITTMANN, O. (1983): Lörrach. Der Naturraum und seine Geschichte. Landschaft, Geschichte, Kultur. 29 pp.; Lörrach (Stadt Lörrach).

WRIGHT, T. (1860): On the Subdivisions of the Inferior Oolite in the South of England, compared with the Equivalent Beds of that Formation on the Yorkshire Coast. – The Quaterly Journal of the Geological Society of London, **16**: 1–48.

ZATOŃ, M. & MARYNOWSKI, L. (2004): Konzentrat-Lagerstätte-type carbonate concretions from the uppermost Bajocian (Middle Jurassic) of the Częstochowa area, South-Central Poland. – Geological Quarterly, **48**: 339–350.

ZATOŃ, M. & MARYNOWSKI, L. (2006): Ammonite fauna from uppermost Bajocian (Middle Jurassic) calcitic concretions from the Polish Jura – biogeographical and taphonomical implications. – Géobios, **39**: 426–442.

ZIETEN, C. H. v. (1830–1834): Die Versteinerungen Württembergs. 102 pp.; Stuttgart (Schweizerbart).

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